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Early Triassic Marine Biotic Recovery: The Predators' Perspective

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Abstract

Examining the geological past of our planet allows us to study periods of severe climatic and biological crises and recoveries, biotic and abiotic ecosystem fluctuations, and faunal and floral turnovers through time. Furthermore, the recovery dynamics of large predators provide a key for evaluation of the pattern and tempo of ecosystem recovery because predators are interpreted to react most sensitively to environmental turbulences. The end-Permian mass extinction was the most severe crisis experienced by life on Earth, and the common paradigm persists that the biotic recovery from the extinction event was unusually slow and occurred in a step-wise manner, lasting up to eight to nine million years well into the early Middle Triassic (Anisian) in the oceans, and even longer in the terrestrial realm. Here we survey the global distribution and size spectra of Early Triassic and Anisian marine predatory vertebrates (fishes, amphibians and reptiles) to elucidate the height of trophic pyramids in the aftermath of the end-Permian event. The survey of body size was done by compiling maximum standard lengths for the bony fishes and some cartilaginous fishes, and total size (estimates) for the tetrapods. The distribution and size spectra of the latter are difficult to assess because of preservation artifacts and are thus mostly discussed qualitatively. The data nevertheless demonstrate that no significant size increase of predators is observable from the Early Triassic to the Anisian, as would be expected from the prolonged and stepwise trophic recovery model. The data further indicate that marine ecosystems characterized by multiple trophic levels existed from the earliest Early Triassic onwards. However, a major change in the taxonomic composition of predatory guilds occurred less than two million years after the end-Permian extinction event, in which a transition from fish/amphibian to fish/reptile-dominated higher trophic levels within ecosystems became apparent.

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Introduction

The evolution of life on earth can be broadly characterized by a continuum of periods of biodiversification, turnover events, and times of crisis where extinction occurred on a large scale, thus allowing us to study biotic and abiotic ecosystem fluctuations throughout the Phanerozoic, the most severe of which were centered around the end-Permian mass extinction [1–6]. To better understand the dynamics involved, it is necessary to consider and evaluate potential food webs directly after extinction events and during the following recovery phases. By occupying the top of the food webs, apex predators are highly susceptible to environmental fluctuations and stress [7,8] and, therefore, they are key for understanding ecosystem recovery after extinction events (see below). However, limited research on Early Triassic top marine predators still obscures the pattern of recovery among higher trophic guilds after the largest mass extinction event in Earth's history near the Permian-Triassic (PT) boundary, about 252 million years ago [1,9,10].

Throughout the last decade, several papers were published that focused on a variety of southern Chinese Triassic biotas and sites of different geological ages, e.g., Chaohu (Anhui Province, late

Olenekian, late Early Triassic), Panxian (Guizhou Province, middle Anisian, early Middle Triassic), Luoping (Yunnan Province, middle to late Anisian), Xingyi (Guizhou, late Ladinian, late Middle Triassic), and Guanling (Guizhou, early Carnian, early Late Triassic), yielding in many cases new taxa and well-preserved marine vertebrate fossils [11–17]. Two of these biota were subsequently used to infer the timing of the marine biotic recovery from the end-Permian mass extinction, proposing that full recovery was not reached until either in the middle Anisian as shown by the Luoping biota [11,18,19], or even later in the Late Triassic with the Guanling biota [15,17].

A recent review article [20], whose aim was to summarize the factors and patterns involved in the biotic recovery from the end-Permian event, follows the previous interpretation that the middle to late Anisian fossil site of Luoping [18,19] represents one of the earliest recovered ecosystems worldwide. The authors thus adhere to the conventional interpretation in which the recovery phase following the PT-boundary is prolonged for up to 8 million years into the Middle Triassic ([21,22] and references therein). In reference to terrestrial ecosystem “disaster faunas”, it was pointed out that species evenness was also very low in the marine realm and that the trophic pyramid was rebuilt step-by-step throughout

the Early Triassic and Anisian by adding new, higher levels [20]. Species evenness is one of the basic parameters of community structure, indicating the abundance of species coexisting in an ecosystem: high species evenness indicates species are evenly abundant, whereas low species evenness shows that some species are more abundant and thus, are dominant over others [23]. On p. 377 [20] it was further noted that in the Luoping biota “[...] the 25 species of fishes and diverse marine reptilians, comprising together 4% of finds, show multiple new predatory levels in the ecosystems [...]”, but they do not explain which of those were supposedly missing in the Early Triassic.

Why is it important to examine the recovery patterns of apex predators (i.e., upper trophic level predators; = top predators) following the end-Permian mass extinction? Studies of modern ecosystem dynamics indicate the crucial role that apex predators play in stabilizing ecosystems, and that the depletion of this guild can cause severe instabilities and loss of biodiversity [7,8]. Conversely, we hypothesize that if apex predators are recovered from a fossil site, their presence would indicate a certain diversity and length of trophic chains in the ancient ecosystems in question (see below). We therefore conducted a comprehensive study of available data for Early Triassic and Anisian larger marine vertebrates (Chondrichthyes, Osteichthyes, Tetrapoda). Our data base includes information on species richness (i.e., fishes: a count of species for which size data are known; reptiles: all species were considered) and body size of osteichthyan and chondrichthyan fishes, as well as secondary marine tetrapods, namely temnospondyl ‘amphibians’ (mainly trematosauroids) and reptiles (e.g., thalattosaurs, ichthyosaurs, sauropterygians). This study aims to elucidate the patterns of spatial and size distribution of key marine predators following the PT-boundary mass extinction as an indicator of the length of food chains or the number of trophic levels. Due to the limited knowledge about body size in Chondrichthyes (fossils are mostly restricted to isolated teeth, fin spines or denticles) their role as marine apex predators is, with some exceptions, qualitatively discussed herein. This group is comprehensively studied elsewhere [24].

Because a study of the biodiversity of secondary marine tetrapods during the Mesozoic [25] investigated the diversity patterns at the stage level but not at the sub-stage or higher resolved biostratigraphic levels (i.e., zones and subzones), these data therefore are only marginally useful herein. Previous evaluations of fish diversity across the Permian-Triassic boundary [26–28], which basically show an increase in diversity following the PT boundary crisis, are also only of limited use for the aim of our study. Although the presented analysis does not adequately assess trophic network complexities [29] for the Early Triassic marine realm, food chain lengths ending with large top-predators nevertheless imply at least stacks of underlying trophic levels (including primary producers, primary and secondary consumers and higher predatory levels) and thus, help to illuminate recovery patterns of marine ecosystems after the end-Permian mass extinction.

Data for the present study are derived from the literature (Fig. 1; Table S1 in File S1), as well as new specimens (Figs. 2, 3). Species relative abundance (e.g. beta diversity), which would be a better measure of biodiversity than pure species counts [30], is more difficult to assess because, in many instances, species abundance has not been quantified, fossils are fragmentary and can only be assigned to higher level taxonomic clades, or the exact location of a particular fossil find is not well known. It is also noteworthy that in the last decade, the Early Triassic time scale has been increasingly refined using combined ammonoid and/or conodont faunas with radiometric dates, thus leading to re-definitions of

Triassic stage and sub-stage boundary ages [9,10,31–34]. For example, in just six years, the Permian-Triassic boundary shifted from 251.0 Ma to 252.2 Ma and the Olenekian-Anisian boundary from 245.0 Ma to 247.2 Ma, respectively [10,35]. Furthermore, index fossils (fossils considered to be characteristic of a certain time period only) are sometimes found to have diachronous first occurrences. Just such a case involved the supposed earliest Anisian-aged conodont *Chiosella timorensis*, a proposed index fossil for the Olenekian-Anisian boundary, which was recently shown to actually overlap in stratigraphic occurrence with Late Spathian ammonoids [36]. A similar case of diachronous first occurrence is also documented for the base of the Triassic with the index conodont species *Hindeodus parvus* [37]. These and other examples of course have implications for the accuracy of the timing of Early Triassic biotic recovery.

Materials and Methods

Institutional Abbreviations

BES, Paleontological collection of the Museum of Natural History of Milan, Italy; BSP, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany; CCCGS, Chengdu Center of China Geological Survey, Chengdu, China; CMC, Cincinnati Museum Center, Museum of Natural History and Science, Cincinnati, Ohio, USA; GMPKU, Geological Museum of Peking University, Beijing, China; GMR, Geological Survey of Guizhou Province, Guiyang, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NMNS, National Museum of Natural Science, Taichung, Taiwan; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; PIMUZ, Paleontological Institute and Museum, University of Zurich, Zurich, Switzerland; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TMP, Royal Tyrrell Museum, Drumheller, Alberta, Canada; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; YIGMR, Wuhan Institute of Geology and Mineral Resources (former Yichang Institute of Geology and Mineral Resources), Hubei Province, China; YPM, Yale Peabody Museum, New Haven, Connecticut, USA; ZMNH, Zhejiang Museum of Natural History, Hangzhou, Zhejiang, China.

The fossil specimen (NMMNH P-65886, ichthyosaur humerus) is stored and curated at the New Mexico Museum of Natural History and Science, 1801 Mountain Road NW, Albuquerque, New Mexico, 87104, USA (NMMNH). It was originally collected on private property before it was donated to the museum, so no collection permits were necessary. The specimen was originally collected from the surface just above Horizon H19 of Guex *et al.* [38] at the Hammond Creek locality (Bear Lake County, SE Idaho), which contains only Spathian-aged marine sediments and ammonoids (*Ceccaiculitoides hammondi*; *Silberlingeria bearlakensis*; *Silberlingeria coronata*; *Silberlingeria sarahjanae*). The age of the humerus, although not found deeply embedded in the rock, is still well constrained based on the fact that a) ammonoids of latest Late Smithian age do not occur in Hammond Creek and b) marine Middle Triassic strata do not occur anywhere in Idaho. The closest marine strata of Middle Triassic age (Middle Anisian) are in central Nevada, over 300 miles further to the S-SW of the Hammond Creek locality.

Specimens PIMUZ 30731 (coprolite) and PIMUZ A/I 4301 (*Birgeria* sp.) are stored and curated at the Paläontologisches Institut und Museum, Universität Zürich, Karl Schmid-Strasse 4, CH-8006 Zürich, Switzerland. The former was collected with

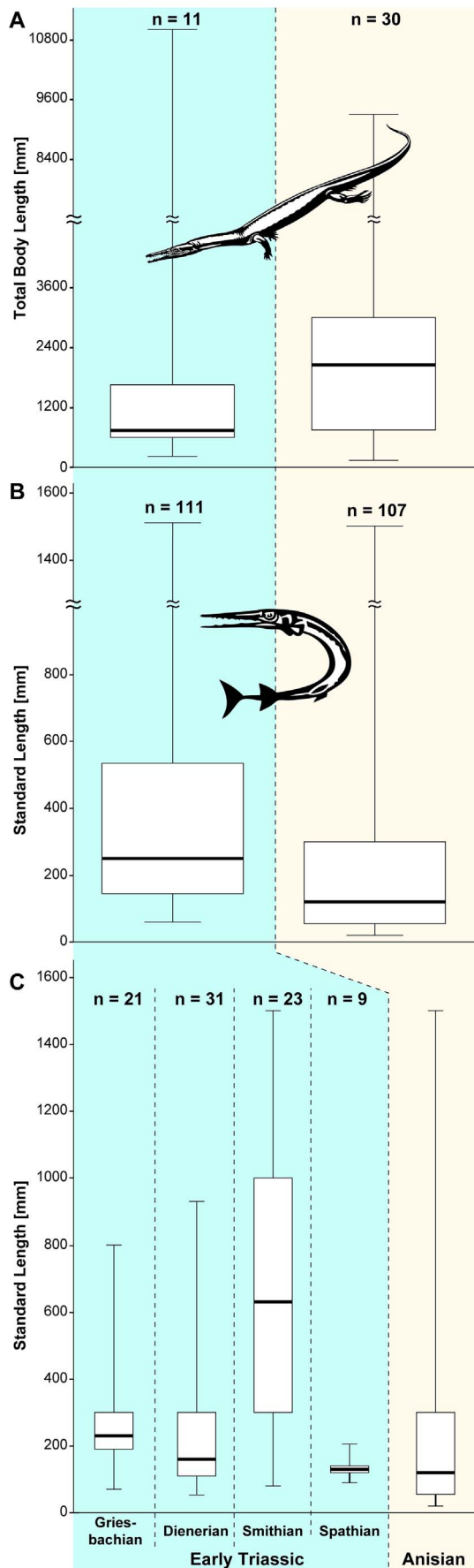


Figure 1. Boxplots showing maximum size (= total body length) of marine tetrapod ('amphibians', reptiles) and maximum standard lengths of marine non-tetrapod vertebrates (osteichthyans, chondrichthyans). A. Tetrapod data for the Early Triassic (11 taxa) and the Anisian (30 taxa). Note that the apparent increase in size is not significant. B, C. Non-tetrapod data comprising marine bony fishes (Actinistia, Actinopterygii) and some chondrichthyans with reliable body size estimates in the Early Triassic and the Anisian (early Middle Triassic). The upper two columns in (B) depict the pooled data, whereas in (C) the Early Triassic is split into the respective sub-stages. Based on data taken from the literature for 111 and 107 species for the Early Triassic and the Anisian respectively (see Table S1 in File S1). The boxes represent the 25–75 percent quartiles (bold horizontal lines indicate the medians) and the width of the tails the whole spread of data.
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Measurements

The maximum standard length (MSL) of marine species of bony fishes (Actinistia, Actinopterygii) and some cartilaginous fishes (Chondrichthyes) of Early Triassic and Anisian (Middle Triassic) age is mainly based on literature data (Fig. 1 and Table S1 in File S1). MSL of Triassic predatory fishes *Birgeria* and *Saurichthys* was in some cases estimated based on available material in comparison with more complete specimens. In general, the skull length of *Saurichthys* usually measures one fourth to one third of the standard length [39,40]. In *Birgeria*, the skull (without pectoral girdle) usually makes up nearly one fifth of the standard length (cf. [41,42]). Where a range is given in Table S1 in File S1, the mean value was used for the box plot analysis (Fig. 1). Where a minimum or maximum length is given (indicated by the > or < symbols), the appropriate number was used for the box plot analyses, assuming that these values approximately represent the size of the fish. With some exceptions (see Table S1 in File S1), MSL in chondrichthyans is difficult to estimate. In higher tetrapod clades (temnospondyl 'amphibians' and reptiles) diversity and size spectra are also difficult to assess because of preservational artifacts. Where appropriate, maximum length (= total size) was measured or estimated based either on the literature or on real specimens, whereas the remainder of the taxa were discussed qualitatively. Note that throughout the article, the term *amphibian* is used in quotation marks to indicate that we refer to extinct stem-amphibians herein and not to crown Lissamphibia.

Fossils were measured (Fig. 2, 3; Table S3 in File S1) with a band scale and calipers or digitally, using the software Fiji [43]. Statistical analyses were performed using the open access software PAST [44].

Results

The Marine Fish Record

Of the various groups of fishes and fish-like basal vertebrates, only four lineages cross the Permian-Triassic boundary: 'Cyclostomata' (hagfishes, lampreys and their fossil relatives; [45]), Conodonts (basal jawless animals with teeth-like elements and controversial systematic affinities; [46–48]), Chondrichthyes (cartilaginous fishes: sharks and their relatives [28]) and Osteichthyes

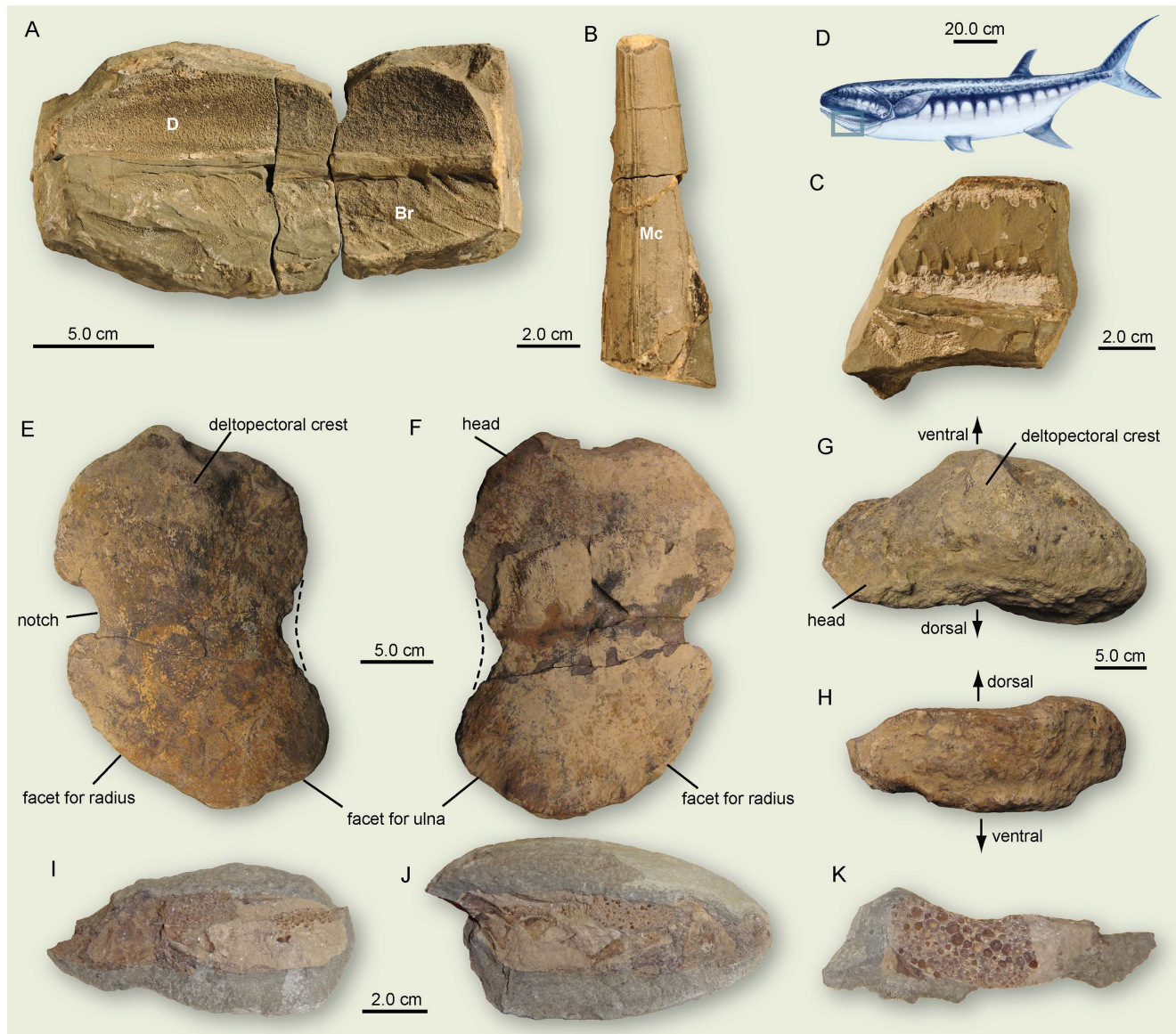


Figure 2. New fossil finds corroborating the presence of large predators in the Early Triassic. A–C. Assemblage of skull and lower jaw elements of a large *Birgeria* sp. (PIMUZ A/I 4301) from the Lusitaniadalen Member (Smithian), Vikinghøgda Formation, Stensiøfjellet, Sassendalen, Spitsbergen. Note that specimen (B) represents the infilling of the Meckelian canal. D. Position of the large specimen (A) on the reconstruction of animal indicated by blue rectangle. E–H. Humerus (NMMNH P-65886) of a giant ichthyosaur from the mid to late Spathian in the Hammond Creek area, Bear Lake valley, southeast Idaho, USA. I–K. Nodule (PIMUZ 30731) containing large coprolite with fish remains from the Griesbachian of Kap Stosch, East Greenland, possibly from a temnospondyl ‘amphibian’. Br, branchiostegal rays; D, dentary; Mc, Meckelian canal (infilling). doi:10.1371/journal.pone.0088987.g002

(bony fishes: lungfishes, actinistians and actinopterygians [28,49]). ‘Cyclostomata’, while generally rare in the fossil record, are not yet known from the Early Triassic. While conodonts undoubtedly represent a major component as both predators as well as prey items in the ancient ecosystems of Permian and Triassic times [50], it is only the cartilaginous and bony fishes (see below) that constituted the large predators among the non-tetrapod vertebrates in the marine realms at that time. Fishes, especially actinopterygians, generally exhibit an increase in diversity at the beginning of the Mesozoic, and reach their first peak in the Middle Triassic [26–28,51,52]. A specific radiation event has been recently proposed for neoselachian and hybodont chondrichthyans at the Permo-Triassic boundary, partly as a response to the extinction of previously abundant Palaeozoic stem chondrichth-

yans (e.g., Stethacanthidae) [53], although some clades such as cladodontomorph chondrichthyans might have survived into the Triassic utilizing deep-sea refugia [54].

In contrast to the southern Chinese localities mentioned above, the classical Early Triassic vertebrate sites in Greenland, Spitsbergen (Arctic Norway), Madagascar and British Columbia (Canada) are characterized by high abundances of fish fossils and diverse ichthyofaunas (e.g. [55–58]; CR & HB pers. obs.). Fishes from these sites exhibit a wide spectrum of shapes and sizes [59] ranging from more general fusiform species like *Boreosomus* Stensiö, 1921 and *Pteroniscus* White, 1933 (= *Glaucolepis* Stensiö, 1921) to deep-bodied forms such as *Bobasatrania* White, 1932, and the garfish-shaped predatory actinopterygian *Saurichthys* Agassiz, 1834.

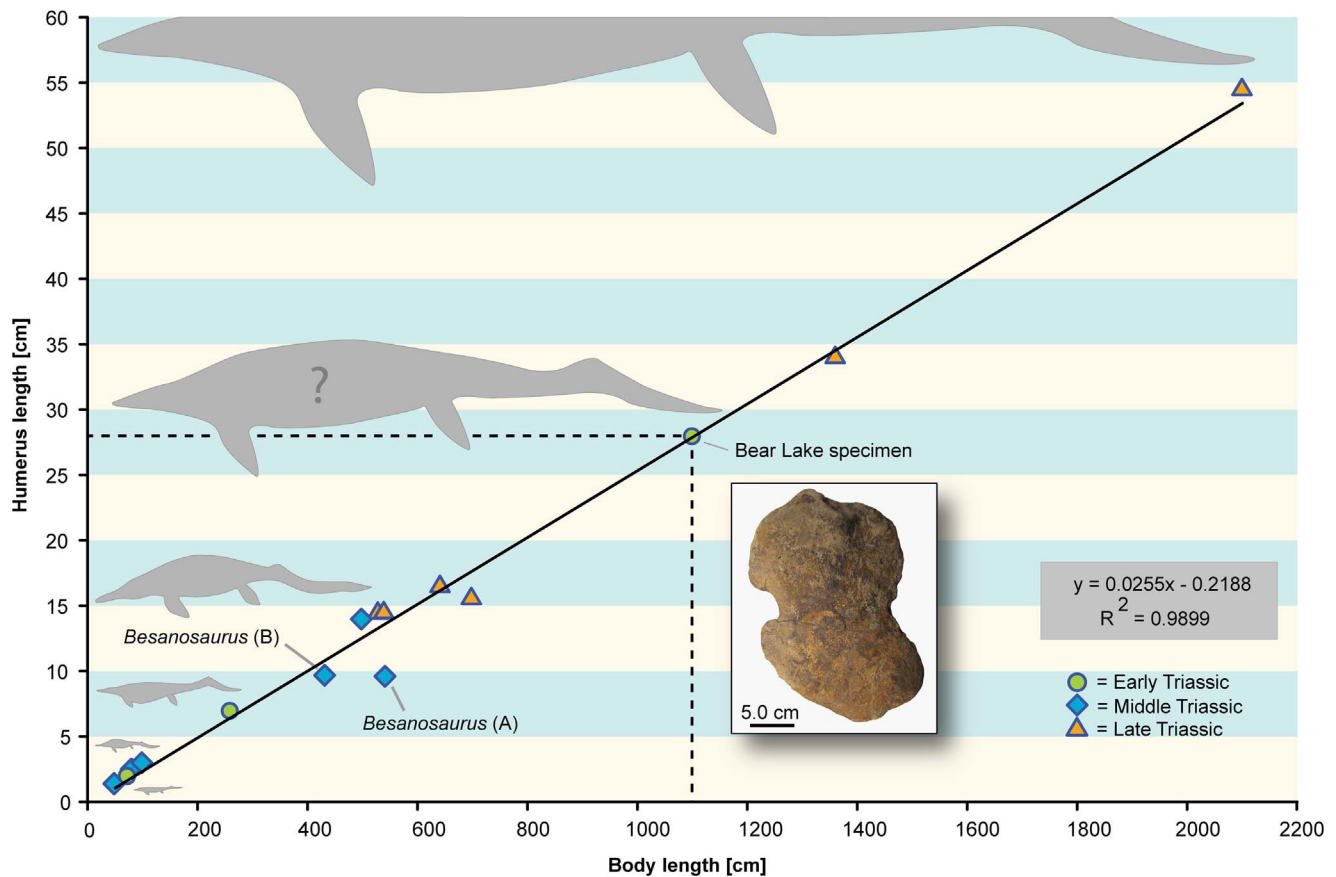


Figure 3. Humeral proximodistal length-body length relation in Triassic ichthyosaurs. Note that the upper two data points (*Shonisaurus popularis* and *Shastasaurus sikanniensis*) are based on estimated body lengths, whereas the other points rely on complete specimens. Removing the two taxa from the plot results in a shift of the specimen from Bear Lake (southwest Idaho, USA) towards even larger body size estimates. doi:10.1371/journal.pone.0088987.g003

Conversely, Early Triassic marine fishes from China are still very poorly known compared to those from the Middle Triassic of this region, and are basically restricted to Chaohu in Anhui Province, Jurong in Jiangsu Province, Zuodeng in Guangxi Province, and Changxing in Zhejiang Province [11,59]. Most of these faunas are of Spathian age [60,61] and include relatively small parasemionotid and “perleidid” actinopterygians, but *Saurichthys* and predatory hybodontoid sharks have also been mentioned ([60,62–66]; see [59] for research history). Most of these faunas have only recently been studied and are still poorly understood. Hence, the Chinese record alone is not suitable for a discussion of global recovery patterns of fishes after the end-Permian mass extinction (*contra* [11,15,18,20]).

We have compiled a record of the maximum standard length (MSL) of marine Actinistia and Actinopterygii (Osteichthyes) and some Chondrichthyes known by more complete fossil remains from the Early Triassic and Anisian (see Table S1 in File S1). Body size in fishes is a proxy for trophic level affiliation, as was recently demonstrated for extant taxa [67,68]. Our results show that marine bony fishes occupied a similar spectrum of body size during the Early Triassic and the Anisian (Fig. 1), ranging from a few centimeters to at least 1.5 meters (Table S1 in File S1). However, in total median MSL of fishes was larger in the Early Triassic than in the Anisian (Mann-Whitney U test, $p < 0.01$) [44]. Moreover, the distribution of MSL was also shifted towards larger body sizes in the Early Triassic compared to the Anisian (Kolmogorov-Smirnov test, $p < 0.01$). Body size changes between

the Early and Middle Triassic are also seen in some families, for instance, Middle Triassic bobasatraniids and actinistians attained MSLs of only a few tens of centimeters and were thus much smaller than some of their Early Triassic relatives that achieved body lengths greater than 1 meter (Table S1 in File S1). Our compiled data representing MSLs of fishes clearly contradict the claim that higher trophic levels were absent from marine ecosystems during the Early Triassic and, thus, refutes the stepwise recovery model of the trophic pyramid [20].

Chondrichthyes. Cartilaginous fishes are usually represented in the fossil record as isolated teeth, dermal denticles, fin spines or cephalic spines. Due to the reduced fossilization potential of cartilage compared to apatite (e.g. bones and teeth), complete body fossils of chondrichthyans are rare. Therefore, data concerning body size of chondrichthyans are relatively sparse (Table S1 in File S1). However, chondrichthyan teeth are often abundant in micro- and macrofossil assemblages and they provide valuable information regarding the dimensions and diet of the animals to which they belonged. The Early Triassic record of Chondrichthyes includes not only predatory forms with tearing-type teeth (e.g., *Hybodus rapax* Stensiö, 1921, with teeth that are at least 23 mm long and 32 mm high), but also durophagous groups (e.g., *Acrodus* Agassiz, 1837, with teeth of up to 24 mm length: [58,69]; *Palaeobates polaris* Stensiö, 1921, with teeth of up to 15 mm length and an estimated body length of ca. 100 cm: [70]). Other possible hybodontoids of Early Triassic age such as *Homalodontus* Mutter, Neuman & de Blanger, 2008 [71] (= *Wapitiodus* Mutter,

de Blanger & Neuman, 2007) also reached large sizes of up to 150 cm [72]. Hybodontoids (*sensu* [73]), one of the dominant group of Mesozoic chondrichthyans, were already widespread at the onset of the Triassic [59]. Neoselachii, the clade that includes all extant chondrichthyans, have been known since the Paleozoic and are also occurring in Early Triassic fossil fish assemblages (e.g., [24,74,75]). Eugeneodontiformes (Fig. 4), a group of Paleozoic “tooth-whorl” bearing chondrichthyans that included such iconic forms as *Helicoprion* Karpinsky, 1899 from the Permian [76], exhibits various tooth morphologies and has its last occurrence in the Early Triassic [24,77,78]. This enigmatic group comprises Early Triassic species ranging from 100 to 150 cm in length (e.g. *Caseodus* Zangerl, 1981, *Fadenia* Nielsen, 1932), similar in size to their Paleozoic relatives [78]. *Fadenia*, for instance, possessed a large, homocercal caudal fin [78] that is typical for fast-swimming, active predators. Eugeneodontiform teeth have been recovered from various world-wide Early Triassic deposits, including western Canada [78], Spitsbergen [79], Greenland [80], Azerbaijan [81,82] and South Tibet [83], thus demonstrating the widespread existence of the group prior to its extinction in the late Early Triassic [24,77].

Another Paleozoic survivor genus is *Listracanthus* Newberry & Worthen, 1870, a chondrichthyan of unknown systematic affinities. This taxon has been described from the Early Triassic of western Canada [56,84], from strata of Smithian or older age. As for the Eugeneodontiformes, *Listracanthus* disappears from the fossil record in the Early Triassic. Although *Listracanthus* is only known from denticles, it was suggested to be of large size and, hence, would classify as yet another chondrichthyan predator of Early Triassic age [84]. Mutter & Neumann [85] speculated that the large denticles of *Listracanthus* could represent gill rakers of a large filter-feeder. However, besides this dubious case, there is no fossil evidence for filter-feeding fishes or tetrapods in the Early Triassic. Furthermore, a lilliput effect was proposed for *Listracanthus* based on changes in denticle size during the Early Triassic [85] in comparison to the older records of the taxon. However, this interpretation seems questionable as changes in size of denticles do not necessarily reflect differences in body size [28].

Osteichthyes. Early and Middle Triassic marine bony fishes include actinopterygians (ray-finned fishes) and actinistians (coelacanths). Dipnoans (lungfishes) were restricted to the freshwater realm (apart from a few possible exceptions; [86]) and are therefore not considered herein. Compared to Chondrichthyes, the potential for fossilization of Osteichthyes is generally higher. Marine bony fishes exhibit an overwhelming diversity of body shapes and sizes during the Early Triassic, including small to mid-sized fusiform taxa (e.g. *Boreosomus*, *Pteronisculus*, *Helmorepis* Stensjö, 1932; Parasemionotidae: [55,57,58,63,64]), small to very large deep-bodied forms (e.g. *Bobasatrania*, *Ecrinesomus* Woodward, 1910: [56,57,87,88]), as well as large fast-swimming predators (*Birgeria* Stensjö, 1919, *Rebellatrix* Wendruff & Wilson, 2012) and small to large ambush predators (*Saurichthys*: [89,90]). It has been shown that many genera achieved a global distribution during the Early Triassic [24,56,59,91].

Actinopterygians, which make up the bulk of bony fishes, had already developed different feeding specializations in the earliest Triassic (Griesbachian). This group includes small to large durophagous forms (Fig. 4; e.g. *Bobasatrania* with pharyngeal tooth plates: [51,57]), as well as mid-sized (e.g., *Pteronisculus*: [55,92]) and large carnivores (Fig. 4; e.g. *Birgeria*, *Saurichthys*: [41,89]). The latter two taxa, *Birgeria* (Fig. 2A–C) and *Saurichthys*, the piscine apex predators of the Triassic [93], retained the same maximum body size of ca. 1.5 meters during the Early and Middle Triassic ([42,58,90,94,95] HB & JJ pers. obs.). Other marine Early Triassic

fishes such as parasemionotids and platysiagids, both of which are known from various paleogeographic regions, remained relatively small (normally below 20 cm) as adults and, thus, would represent lower trophic levels [55,57,96].

Birgeria and *Saurichthys* are known at least from the Griesbachian onwards [57,89], and both taxa exhibit a cosmopolitan distribution during the Early Triassic [42,97]. Although *Saurichthys* fossils are relatively sparse in the Early Triassic of East Greenland (14 specimens [89]), remains of *Birgeria* are quite common (107 specimens [41]) in this region. *Birgeria* and *Saurichthys* are also known from abundant material from the Early Triassic of the USA and Canada (ca. 52 specimens of *Saurichthys*: [56,95,97]; *Birgeria* is rare) and Spitsbergen (59 specimens of *Saurichthys*: [90], and nine of *Birgeria*: [58,90]). Although only a few specimens of *Birgeria* and *Saurichthys* from Madagascar have so far been mentioned in publications [55,98–102], well over 100 additional yet undescribed individuals of *Saurichthys* are distributed in museum collections (e.g. Paris, Freiberg, Zurich; CR pers. obs., I. Kogan pers. comm. to CR). Taking sampling bias (see below) into account, these numbers are comparable with the Middle Triassic record: e.g. at least 67 specimens of *Birgeria* and about 320 individuals of *Saurichthys* from Monte San Giorgio area, southern Switzerland and northern Italy [40,42], and more than 150 specimens of *Saurichthys* (including *Sinosaurichthys* Wu, Sun, Hao, Jiang, Xu, Sun & Tintori, 2011) from southern China [103–105]. Hence, at the global scale *Birgeria* and *Saurichthys* cannot be considered rare in the Early Triassic (contra [20]: p. 379).

Actinistians, which show generally low diversity in the fossil record, achieved their all-time highest diversity during the Early Triassic, with at least 13 valid genera ([97,106] and references therein). This group includes small to mid-sized taxa (e.g. *Piveteaunia* Lehman, 1952: [55,107], *Chaohuichthys* Tong, Zhou, Erwin, Zou & Zhao, 2006 [64], *Belemnocerca* Wendruff & Wilson, 2013 [106]), as well as very large forms. For example, a body length of 600–800 mm has been estimated for *Mylacanthus* Stensjö, 1921 and *Wimania* Stensjö, 1921 from the Smithian of Spitsbergen ([58]) and the recently discovered *Rebellatrix* (Fig. 4) from the Early Triassic of western Canada reached an estimated length of 1300 mm [108]. Some Early Triassic actinistians were fast-swimming predators (*Rebellatrix*), while others (e.g., *Axelia*, *Mylacanthus*) had a slow-moving benthos-oriented lifestyle and a durophagous diet ([57,58,108]).

The Marine Tetrapod Record

Among Tetrapoda, temnospondyl ‘amphibians’, procoplophoid parareptiles, eutherapsid synapsids (anomodonts and eutheriodonts, the latter leading to modern mammals), and basal eureptiles (which later gave rise to modern reptile groups like lizards, snakes and crocodylians) survived the Permian-Triassic extinction event [5,109–115]. Of these groups, only the temnospondyl ‘amphibians’ and eureptiles (e.g. ‘younginiform’ eureptiles, protorosaurian archosauromorphs) include species that are adapted to marine life.

Previous studies [116–118] have already noted that the marine reptile diversity seen in the Spathian implies an even older, as yet unrecognized evolutionary record from ancestors with an amphibious lifestyle, and they also pointed out the importance of reptiles for Mesozoic marine ecosystems. These studies, however, were published either before or they did not take into account the latest taxonomic descriptions and revisions of marine reptiles available to date [119–122]. A recent summary of Chinese Triassic marine biota indeed similarly implies early diversification of marine reptiles throughout much of the Early Triassic and even close to the Permian-Triassic boundary [11]. Walker & Brett [123] further summarized patterns of predation both among marine

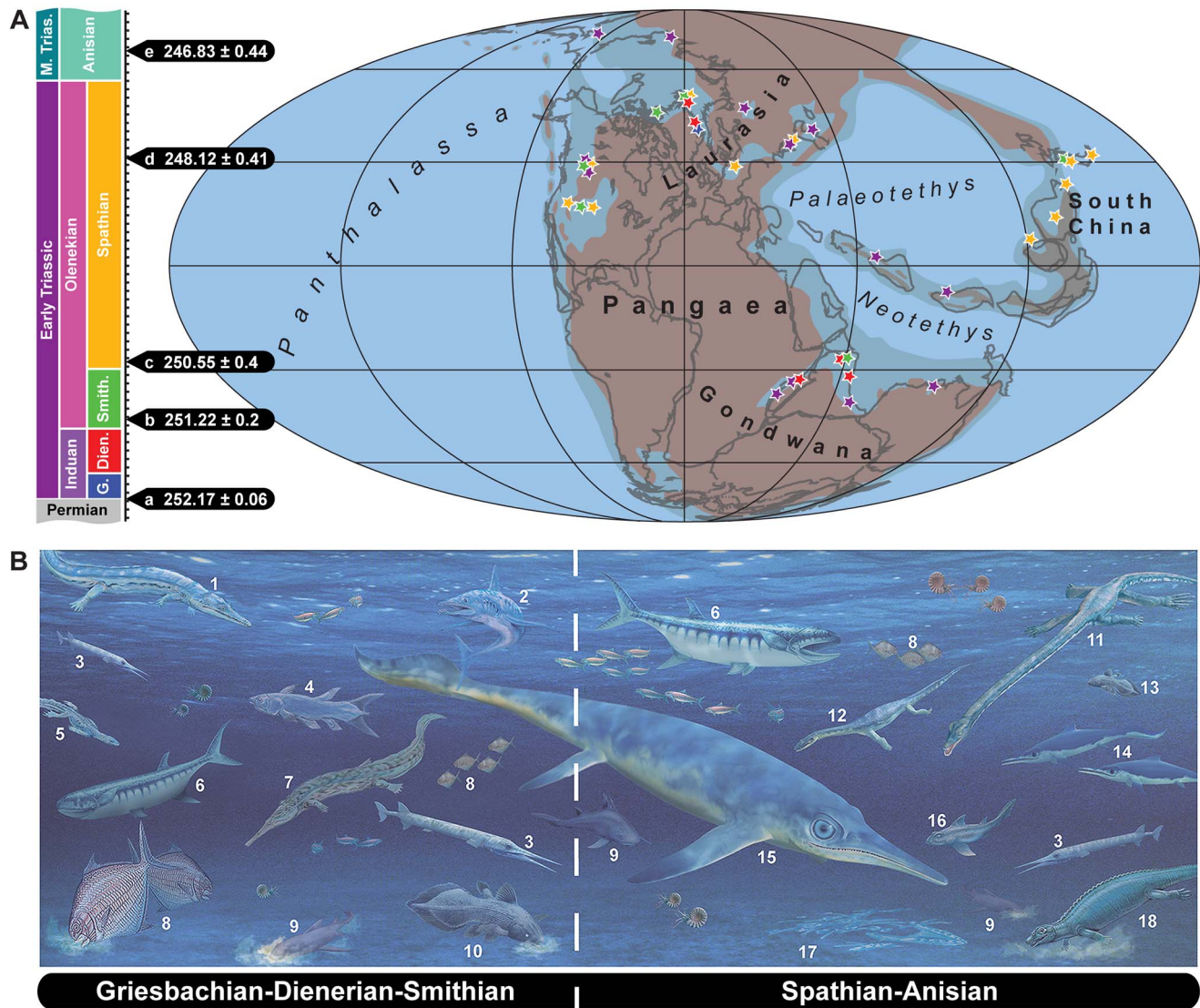


Figure 4. Spatial and stratigraphical distribution of Early Triassic and Anisian (early Middle Triassic) marine vertebrate predators. A. Geological time scale (Permian-Middle Triassic) with absolute time calibration according to radiometric UPb ages: a based on [9]; b on [34]; c–e on [33]. Paleogeographical distribution of selected marine predatory vertebrates is given on the right using the same color code as in the geological time scale (globe modified from C. Scotese's paleomap project; <http://www.scotese.com>). **B.** Marine vertebrate apex predators during the Griesbachian to Smithian interval (left) and the Spathian to Anisian interval (right). Predators not exactly to scale; see text and Tables S1–S2 for details on body size and stratigraphic occurrence. Marine vertebrate apex predators: 1, *Wantzosa* (trematosaurid 'amphibian'); 2, *Fadenia* (eugeneodontiform chondrichthyan); 3, *Saurichthys* (actinopterygian ambush predator); 4, *Rebellatrix* (fork-tailed actinistian); 5, *Hovasaurus* ('younginiform' diapsid reptile); 6, *Birgeria* (fast-swimming predatory actinopterygian); 7, *Aphaneramma* (trematosaurid 'amphibian'); 8, *Bobasatrania* (durophagous actinopterygian); 9, hybodontoid chondrichthyan with durophagous (e.g. *Acrodus*, *Palaeobates*) or tearing-type dentition (e.g. *Hybodus*); 10, e.g., *Mylacanthus* (durophagous actinistian); 11, *Tanystropheus* (protorosaurian reptile); 12, *Corosaurus* (sauropterygian reptile); 13, e.g., *Ticinepomis* (actinistian); 14, *Mixosaurus* (small ichthyosaur); 15, large cymbospondylid/shastasaurid ichthyosaur; 16, neoselachian chondrichthyan; 17, *Omphalosaurus* skeleton (possible durophagous ichthyosaur); 18, *Placodus* (durophagous sauropterygian reptile). Printed under a CC BY license, with permission from Nadine Bösch and Beat Scheffold, original copyright [2013]. doi:10.1371/journal.pone.0088987.g004

vertebrates and invertebrates throughout large parts of the Phanerozoic. An overview of Triassic marine reptiles was recently provided [124], in which the authors note that rates of sea-level changes may have been an important factor influencing nearshore marine ecosystems and thus the evolution and selective extinction of secondary marine reptiles during the Triassic. In this respect, it is worth noting that the Smithian-Spathian boundary has long been recognized as a regression peak [125].

The oldest remains of Tanystropheidae, a group of protorosaurian archosauriforms that included iconic forms such as

Tanystropheus Meyer, 1852 (Fig. 4) with extremely elongated neck vertebrae [126–128], were recently described from the late Early Triassic of the Volgograd Region, western Russia [129], thus constituting yet another, highly specialized predator in the Early Triassic. Whether Hupehsuchia, a group of diapsid reptiles that may be closely related to ichthyosaurs [130], is present as well in the Early Triassic remains under discussion (see below). Of the marine reptile groups studied, the ichthyosaur fossil record in particular yielded many large to enormously large but disarticulated body fossils of late Early Triassic age, as demonstrated for

example by the discovery of a giant humerus from the mid-late Spathian of the Thaynes Formation (Idaho, western USA, Figs. 2D–G, 3). This occurrence supports the hypothesis that ichthyopterygians experienced a burst of diversification and adaptive radiation [131] well before the Middle Triassic. A list of tetrapod species surveyed herein is presented in Table S2 in File S1.

Temnospondyl ‘Amphibians’ (Mainly Trematosauroida). Stereospondyli are a widespread group highly nested within temnospondyl ‘amphibians’, which are known to occur from the Late Permian to Early Cretaceous. Whereas most stereospondyls probably inhabited freshwater lake and river habitats, the trematosauroids are the lineage of temnospondyls considered to have been most successful entering the marine realm [132,133], often showing extremely elongated gharial-like skulls with numerous pointed teeth, implying a piscivorous diet [134–137]. Most trematosauroids were small to medium-sized predators ranging between one and two meters of total body length [122]. The skull of *Wantzosaurus elongatus* Lehman, 1961 ([137]: Fig. 4B) could reach 40 cm in length.

Specimens of trematosauroids, e.g., *Aphaneramma kokeni* Welles, 1993 [138], from the Salt Range of Pakistan are already known from the “*Prionolobus* beds”, Mittiwali Member, Mianwali Formation at Chiddru (e.g., [139,140]), previously identified as either Griesbachian [141] or latest Dienerian [138]. Based on the newest detailed work on ammonoid faunas from the Salt Range, the so-called “*Prionolobus* beds” (= Ceratite Marls) at Chiddru are actually early Smithian in age [6] (*Wantzosaurus* Lehman, 1955, on the other hand, is known from older (Griesbachian?) sediments of Madagascar (Fig. 4A; [122,138]). A rich temnospondyl fauna (an ‘amphibian’ fauna first studied in the 1930s by Sæve-Söderbergh [142], who noted 40 specimens) from the ‘Stegocephalian zone’ and underlying ‘fish zones’ [143] of the Wordie Creek Formation of central East Greenland was reported [144], which is most likely Dienerian in age ([145,146], HB pers. obs.). However, the taxonomic status of many of the originally described Early Triassic species from Greenland largely remains obscure [137,144]. Three genera from the Wordie Creek Formation at Kap Stosch in East Greenland are considered valid ([122,144], see also [147]): the capitosauroid *Aquiloniferus* Bjerring, 1999 (based on material that was previously referred to species of *Luzocephalus* Shishkin, 1980), the trematosaurid *Stoschiosaurus* Sæve-Söderbergh, 1935 and the wetlugasaurid trematosauroid *Wetlugasaurus* Riabinin, 1930.

Research on the temnospondyl fauna of Spitsbergen preceded that of Greenland, starting with the works of Carl Wiman [133,148,149]. In addition to the non-trematosauroid basal stereospondyl *Peltostega* Wiman, 1916 (Rhytidostea), at least five trematosauroid genera are recognized in the ‘Fish Niveau’ (Lusitaniadalen Member) of the Vikinghøgda Formation (= Sticky Keep Formation) of Spitsbergen (Smithian, [150]), namely the trematosaurids *Aphaneramma* Woodward, 1904, *Lyrocephalus* Kuhn, 1961 (= *Lyrocephalus* Wiman, 1913), *Platystega* Wiman, 1914, and *Tertrema* Wiman, 1914, as well as the wetlugasaurid *Sassenisaurus* Nilsson, 1942 [122,133,151,152]. It is noteworthy that the latter four taxa exhibit shorter, more triangular cranial shapes as opposed to the extremely longirostrine skull of *Aphaneramma* (Fig. 4).

Recently published data [153] demonstrated that both trematosaurid subgroups, the shorter-snouted Trematosaurinae and the longer-snouted, gharial-like Lonchorhynchinae, were already present in the earliest Triassic (Griesbachian) and that trematosauroids had already achieved global distribution by that time [122,154]. Hammer [154] hypothesized that trematosaurids are

euryhaline predatory animals that preferred nearshore marine to distal deltaic habitats, based on the associated invertebrate faunal elements such as ammonoids and bivalves. A recent study concerning the bite-forces of temnospondyls further corroborated that within the trematosaurids, long-snouted forms such as *Wantzosaurus* and *Aphaneramma* were fully aquatic and preyed upon fast animals such as small fishes [155], and in the case of the former, a pelagic lifestyle has even been proposed [137]. Dwellers preferring a more coastal/near shore marine habitat may be represented by *Erythrobatrachus* Cosgriff & Garbutt, 1972 from the Upper Blina Shale (Olenekian) of West Kimberley, Western Australia, and *Cosgriffius* Welles, 1993 from the Wupatki Member, Moenkopi Formation (Spathian) of Arizona, USA [122]. It is noteworthy here that pelagic trematosauroids are known only from the Griesbachian to Smithian interval, and their almost complete disappearance from the fossil record roughly coincides with the first stratigraphic appearance of ichthyosaurs and sauropterygians (see below).

Furthermore, a whole range of non-trematosauroid temnospondyls is known from the Early Triassic of northwestern Madagascar [156,157]. These animals are thought to be euryhaline, and at least the capitosaur *Edingerella madagascariensis* (Lehman, 1961) from the Ankitokazo Basin is thought to have also dwelled in brackish to coastal, shallow marine habitats [157–159]. Bone histology of the armour elements of other non-trematosauroid temnospondyls underscores the ability of temnospondyls to tolerate changes in salinity and thus the assumption that they may have entered brackish or near-coastal marine habitats at least during short term hunts, even if they are not considered fully marine [160].

Sauropterygia. Sauropterygia, the widely distributed, diverse group of marine diapsid reptiles that gave rise to the Jurassic-Cretaceous plesiosaurs and pliosaurs is first reported from the Early Triassic. The earliest occurrence of the group is documented by the European record of non-diagnostic sauropterygian remains (Sauropterygia indet.), as well as *Corosaurus alcovensis* Case, 1936 from the Alcova Sandstone of Wyoming, USA [121,161,162]. Accordingly [121,163], the earliest sauropterygian remains from both Europe and North America are of Spathian age (= late Early Triassic; in the Germanic Triassic: lower Röt Formation, upper Buntsandstein). Slightly younger remains referable to *Cymatosaurus* Fritsch, 1894 and *Dactylosaurus* Gürich, 1884 are known from the upper Röt Formation and the lower Muschelkalk of the Germanic Triassic, which is Aegean (early Anisian, Middle Triassic) in age.

Another early sauropterygian is the poorly known *Kiwangisaurus orientalis* Young, 1959 from the “[...] Loulou Group of the Beisi Formation upper Lower Triassic (lower Middle Triassic by some estimates)” of Guangxi Province, China ([164]: p. 325). The Early Triassic Luolou Formation is a mixed carbonate-siliciclastic formation deposited on the outer platform indicating moderately deep water settings, whereas the Beisi Formation is composed of limy mudstones, massive oolite grainstones and dolostone deposits in a shallow marine setting [165,166]. The sauropterygians *Hanosaurus hupehensis* Young, 1972 (note that in the analyses of [167] *Hanosaurus* was recovered outside of Sauropterygia) and *Keichousaurus yunnanensis* Young, 1965, together with hupesuchian remains (see below), have been reported from the Jialingjiang Formation of Wangchenkang (Yuan’an County, Hubei Province [168]), but the age of these fossils is still debated (either late Early Triassic or early Middle Triassic; [169,170]). Accurate dating of these fossils is further complicated due to problems of the ill-defined Olenekian-Anisian boundary by means of conodont datums [36] (see also above).

With regard to the holotype of *C. alcovensis*, Storrs [171] provided a reconstructed skull length of slightly less than 15 cm and an estimated overall body length of 1.65 m. Isolated material (e.g. humerus YPM 41032) referable to *Corosaurus*, suggests the presence of larger individuals more than 4 meters in total length, thus exceeding most of the Middle and Late Triassic non-pistosauroid sauropterygians, including the huge predator *Nothosaurus giganteus* Münster, 1834 from the Germanic Muschelkalk sea and Alpine region [121] (*Paranotosaurus amsleri*, a junior synonym of *N. giganteus*, from the UNESCO World Heritage Site of Monte San Giorgio, Switzerland, has an estimated body length of 3.85 m; [172]).

The durophagous placodonts (Fig. 4) are a specialized Triassic group of sauropterygians that includes both non-armoured and armoured species, of which the latter superficially resembles turtles (e.g., [173,174]). Even though the earliest placodont fossils (i.e., *Placodus* Agassiz, 1833) were recovered from early Anisian sediments [121,161], it is assumed that their evolutionary history reaches back into the late Early Triassic due to the high degree of aquatic adaptation noted in the earliest representatives of this clade [175]. Recently, new placodontiform reptiles [167,176] were described from the lower Muschelkalk (Vossenveld Formation, early Anisian) quarry of Winterswijk, The Netherlands, including a tiny skull of a juvenile sauropterygian reptile, *Palatodonta bleekeri*, which in a phylogenetic analysis [167] was recovered as the direct sister taxon to Placodontia. It shared characters such as a single row of palatine teeth with Placodontia, but lacked any form of crushing dentition. Its basal morphology and place of recovery further argue for an origination of the group in Europe. The highly modified crushing dentition of placodonts [123,177–180], as well as that of other durophagous marine vertebrates in the Early and Middle Triassic, indicates the importance of the crushing guild in the food web; also the diversity of these groups provides a proxy for the rate of sea-level changes during the Triassic period [124].

The discovery of new sauropterygian remains, besides possibly more basal diapsid remains, in the Middle to Upper Member of the Nanlinghu Formation in Majiashan, Chaohu, Anhui Province, southern China [169,170], underscore the fact that the early evolution of the Sauropterygia as a whole is still largely obscured and that its origin definitely dates well back into the Early Triassic. These new sauropterygian fossils, which are contemporaneous with the ichthyopterygian *Chaohusaurus geishanensis* Young & Dong, 1972 (see below), argue directly and indirectly for the presence of placodonts in the Early Triassic, based on skeletal affinities to other known placodonts and through ghost lineage inference.

Thalattosauriformes. Thalattosaurs are a less diverse group of small to medium-sized (generally less than 4 meters in length) secondary marine reptiles restricted to the Triassic (Müller, Renesto & Evans, 2005). The oldest record of the group comes from the name-giving genus, *Thalattosaurus*, whose type species, *T. alexandrae* Merriam, 1904, was first described from the Carnian *Trachyceras* beds of the Hosselkus Limestone of Shasta County, California, USA [181]. Nearly one century later, newly discovered *Thalattosaurus* material from the Lower to Middle Triassic Sulphur Mountain Formation, Wapiti Lake area, British Columbia, Canada, was described as *T. borealis* [182,183]. Material representative of two other taxa, *Paralonectes merriami* Nicholls & Brinkman, 1993 and *Agkistrognathus campbelli* Nicholls & Brinkman, 1993, was also recovered from the Sulphur Mountain Formation in British Columbia [183,184]. All three taxa belong to the monophyletic clade Thalattosauridae within Thalattosauria (Thalattosauria and Askeptosauroidae are then combined into Thalattosauriformes: [185,186]). Because many of the Canadian

specimens were discovered as float in loose scree material on steep slopes [183], it is not possible to assign an exact age to these particular fossils. Nevertheless, specimens of *Paralonectes* and *Agkistrognathus* were found in a location (“cirque D”) where the sedimentary sequence extends from the Olenekian to the Middle Triassic [183].

Ichthyopterygia. Although the record of early ichthyosaurs is still very limited, it is apparent that at least since the Spathian (late Olenekian, late Early Triassic, Fig. 4A), the Ichthyopterygia as a group had already diversified and achieved global distribution, as revealed by discoveries from Asia, North America and northern Europe [119,120,187–193].

McGowan & Motani [120] recognized five well-known Early Triassic species of non-ichthyosaurian ichthyopterygians, namely *Chaohusaurus geishanensis* Young & Dong, 1972, *Grippia longirostris* Wiman, 1929, *Parvinatator wapitiensis* Nicholls & Brinkman, 1995, *Thaisaurus chonglakmanii* Mazin, Suteethorn, Buffetaut, Jaeger & Helmcke-Ingavat, 1991, and *Utatsusaurus hataii* Shikama, Kamei & Murata, 1978 ([194–198]). In addition, another grippidian ichthyosaur, *Gulosaurus helmi*, was recently described [199] based on material from the Vega-Phroso Siltstone Member (Early Triassic), Sulphur Mountain Formation, British Columbia, previously identified either as belonging to *Grippia* cf. *G. longirostris* [200] or to a juvenile specimen of *Parvinatator* [201].

Following the most recent work [202], *Omphalosaurus* Merriam, 1906 (Fig. 4), a durophagous marine reptile with a peculiar crushing dentition consisting of hundreds of stacked, bulbous teeth [202], can also be included within non-ichthyosaurian ichthyopterygians. Of these six taxa, only *C. geishanensis*, *G. longirostris* and *U. hataii* can be accurately dated (late Early Triassic), based on conodont and/or ammonoid age control [120], whereas *Omphalosaurus* is known from the Spathian to the early Ladinian (late Middle Triassic [202]). In the other cases the age control was rather loose and often the remains were found as surface float in assemblages of mixed ages.

P. wapitiensis is known from the Lower to possibly Middle Triassic Sulphur Mountain Formation of Wapiti Lake region, east central British Columbia (Canada) but fossils are usually recovered from loose slabs without further age control [120,195].

G. longirostris was found in the “*Grippia* niveau”, the lower of the two tetrapod-bearing horizons in the upper Vikinghøgda Formation of Spitsbergen [203]. Both horizons belong to the latest Spathian *Keyserlingites subrobustus* Zone ([204] [120], which corresponds to the upper part of the Vendomdalen Member of the Vikinghøgda Formation, Sassendalen Group (*sensu* [205]). Several similarities in the dentition of *G. longirostris*, whose dentition was referred to the crunch guild [206], and *U. hataii* from Japan have been pointed out [207,208]. A revision of the Svalbard ichthyopterygian fauna was recently provided [209] (also see below).

U. hataii is known from the Spathian Osawa Formation of Miyagi, Japan [120,210], and material from the Sulphur Mountain Formation may also be referable to this genus [211]. This taxon was originally described from two profiles (Tatezaki and Osawa) in the Osawa Formation [196]. Dating of these fossils remains difficult, however. Only the upper *Utatsusaurus* occurrences in the profiles can unambiguously be correlated with the *Subcolumbites* Zone (e.g. through the occurrence of *Subcolumbites perinismithi*, *Stacheites* sp., etc.). As for the findings in the lower part of the Tatezaki profile, the ammonoid correlation is incorrect, because, for instance, the older *Columbites parisianus* is mutually exclusive with the younger *Subcolumbites* or *Stacheites* [38]. The faults shown in the Tatezaki profile may further indicate repetition of sedimentary stacks, so that several specimens (A–D and L in [196])

cannot be precisely dated. The oldest, well-dated *Utatsusaurus* material thus appears to be restricted to the middle Spathian (*Subcolumbites* Zone; [212]), which makes it slightly older than the previously assumed late Spathian age [120].

C. geishanensis, one of the smallest forms, was found in the Spathian Qinglong Formation (*Neospathodus triangularis* conodont Zone and *Subcolumbites* Zones) of Anhui, China [213,214]. Its total body length is usually less than 1 meter, and it is regarded as one of the taxa unifying most of the plesiomorphic traits among ichthyosaurs [214]. New material of *Chaohusaurus* (more than eighty specimens by now) has recently been excavated from the Middle to Upper Member of the Nanlinghu Formation (Spathian) in Majiashan, Chaohu, Anhui Province [169,170]. In addition, a new species of *Chaohusaurus*, *C. zhangjiawanensis*, was only recently described from the Jialingjiang Formation (*Neospathodus homeri-N. triangularis* conodont zone) of Yuanan, Hubei Province in South China [215]; the same formation that also yielded for example material of *Hupesuchia* (see below).

Omphalosaurus (type species: *O. nevadanus*), ([119,202,216,217] was originally described from the late Early and Middle Triassic Prida Formation (Fossil Hill Member), Humboldt Range, Nevada, USA [190,218]. Associated cranial and postcranial remains of *Omphalosaurus* cf. *O. nevadanus* (originally described as *O. wolfi*: [219]) are now known from the Middle Triassic (earliest Ladinian) of the Salzburg Alps, Austria, close to the German border [202,220] and it showed affinities of the taxon to ichthyosaurs (but see [120] for different interpretation). Its lower jaw, which may have carried hundreds of rounded crushing teeth of various sizes, would exceed 50 cm in length if reconstructed [202]. The earliest records of this durophagous animal were described as *O. nettasthynchus* [190] already from the late Spathian (*Neopopanoceras haugi* Zone, Lower Member of the Prida Formation [218] of the Humboldt Range).

In addition to these better known basal ichthyopterygian species, representatives of more derived groups (e.g., mixosaurs, shastasaurids) which later flourished in the Middle and Late Triassic are also fragmentarily known from the late Early Triassic [120,189,221]. The shastasaurids in particular include large to giant-sized ichthyosaurs.

None of these early ichthyopterygians show the characteristic parvipelvic (meaning with a “small pelvis”) body shape of later ichthyosaurs, but instead had an elongate lizard-like body shape, an anguilliform (eel-like) mode of swimming, and they did not exceed three meters in total body size, with most species being smaller than one meter [214,222].

The heterodont dentition found in many Early and Middle Triassic non-ichthyosaurian and ichthyosaurian ichthyopterygians (e.g., mixosaurs: [223], *Grippia*: [208]) may be indicative of a more omnivorous diet in these taxa [224]. A recent phylogenetic study indicates that *Xinminisaurus* Jiang, Motani, Hao, Schmitz, Rieppel, Sun & Sun, 2008, a form with crushing dentition from the Upper Member of the Guanling Formation at Panxian, Guizhou Province, China [225], might have had a ghost-range into the late Early Triassic as well [193].

The diverse ichthyopterygian fauna of the Svalbard archipelago was recently reviewed by Maxwell & Kear [209], who recognized six valid genera: *Grippia* Wiman, 1929, *Quasianosteosaurus* Maisch & Matzke, 2003, *Pessopteryx* Wiman, 1910 [226], *Omphalosaurus* Merriam, 1906, *Isfjordosaurus* Motani, 1999 and an additional indeterminate ichthyopterygian. *Isfjordosaurus minor* (Wiman, 1910) [226] and species of *Pessopteryx* Wiman, 1910 (including “*Rotundopteryx*” *hulkei* Maisch & Matzke, 2000 *sensu* [120]), which are also based on limited postcranial material from the “lower saurian niveau” (Vendomedalen Member) of the upper Vikinghøgda

Formation of Spitsbergen, were treated as *species inquirendae* and *nomina dubia* respectively [120]. Later, a new genus name *Merriamosaurus* Maisch & Matzke, 2002 was introduced based on material of “*Rotundopteryx*” *hulkei* from the MNHN collections in Paris, France, which led to recognition and description of associated postcranial remains of a single individual among the otherwise isolated material [227,228]. The taxon was described as a large species, which occupies “[...] the most basal position in Merriamosauria, forming the sister-group to *Besanosaurus* and all other more highly derived merriamosaurs” ([228]: p. 133). Following Maisch [188] and Maxwell & Kear [209], *Merriamosaurus hulkei* is herein treated as a junior synonym of *Pessopteryx nisseri* Wiman, 1910, a large ichthyosaur with shastasaurid affinities.

Furthermore, large teeth (more than 40 mm in length) from nodules at the base of the Spathian “*Grippia* niveau” were described as *Svalbardosaurus crassidens* [229,230]. According to Maxwell & Kear [209], these teeth belonged to a large ‘amphibian’ rather than an ichthyosaur. Regardless of their systematic interpretation, these teeth still indicate the presence of very large predator in the Early Triassic of Spitsbergen. On the other hand, *Omphalosaurus*-like teeth were found among the material originally assigned to *Pessopteryx*. *Quasianosteosaurus vikinghøgda*, an ichthyosaur whose skull length at least reached 50 cm, was also described from the lowermost “*Grippia* niveau” of the Vikinghøgda Formation [131]. According to these authors, *Quasianosteosaurus* anatomy compares closely to that of *Parvinator*, with both classified as non-ichthyosaurian ichthyopterygians.

Recently, still undescribed ichthyosaur fauna was reported from the Fossil Hill locality, Prida Formation, of Pershing County, Nevada [231]. The discoveries were derived from Spathian-aged layers, similar to those from which *O. nettasthynchus* was described [190]. Preliminary tooth morphology studies indicate that an “*Utatsusaurus*-like form, and a *Chaohusaurus*/*Grippia*-like form” ([231]: p. 120) are among the new fossils. These taxa are more or less well-known from Canada, China, Japan, and Spitsbergen.

Material that was thought to represent *Cymbospondylus* Leidy, 1868 (several vertebrae, a distal portion of a left humerus, and some indeterminate bone) were described from the Olenekian Thaynes Formation at Nounan Valley, west of Georgetown, Bear Lake County, Idaho ([232,233]; note that the morphological characters thought to be diagnostic for the genus by Massare and Callaway are not valid anymore, see [120]). As surface float collections within limestone nodules, these bones derived from the shales below the Platy Siltstone Member [232] from sediments of either Smithian or early Spathian age (see also [233]).

A new, unusually large ichthyosaur humerus (NMMNH P-65886, Fig. 2D-G) about 28.0 cm in proximodistal length that was also recently recovered from the mid-late Spathian portion (*Subcolumbites* Zone, biochronologic horizon 18 of [38]) of the Thaynes Formation (Hammond Creek, Bear Lake County, Idaho, USA), rivals the dimensions of some of the largest ichthyosaurs known. It is exceeded only by shastasaurids such as *Shonisaurus popularis* Camp, 1976 (maximum humeral length 43 cm; [234]) from the upper Carnian (Late Triassic) of Nevada, USA, and the gigantic *Shastasaurus sikanniensis* (nov. comb. by [235]; originally described as *Shonisaurus sikanniensis* in [234]) from the Late Triassic of British Columbia, which is estimated to have reached up to 21 m in total body length and whose humerus measured an amazing 54.5 cm in proximodistal length [234]. A highly predatory species, *Thalattoarchon saurophagis*, with flattened cutting-edged teeth from marine sediments of Middle Triassic age, Augusta Mountains, Pershing County, Nevada, was also estimated to have reached more than 8.6 meters in body length [236]. The

new humerus from Hammond Creek resembles the deeply notched humeri of certain Late Triassic ichthyosaurs, fitting humerus morphotype 2 *sensu* [237], which is characteristic for Shastasauridae Merriam, 1902. It most closely resembles the deeply notched humerus of *Callawayia neoscapularis* (McGowan, 1994) from the Late Triassic Pardonet Formation of British Columbia ([119,120], see also [237,238]) or *Shastasaurus pacificus* (*sensu* [120]; for “*Shastasaurus altispinus*”: [239]). According to the analyses of Sander *et al.* ([235]) and Fröbisch *et al.* [236], *Callawayia* was not a shastasaurid, but instead more highly nested among the more advanced parvipelvian ichthyosaurs, the clade which is characterized by a different humerus shape, i.e., morphotype 3 *sensu* [237]. Motani [237] conceded, however, that a few taxa (e.g., *Cymbospondylus* and *Toretocnemus* Merriam, 1903 at the time) do not fit their proposed morphotype classification. Other recent phylogenetic analyses [199,240], using updated versions of the data matrices of Motani [130] and Thorne *et al.* [193] and centering on the reinterpretation of grippid material from the Sulphur Mountain Formation, British Columbia, as well as of *Utatsusaurus* from Japan, recovered *Callawayia* again in a more classical position in a clade with *Shastasaurus* and *Shonisaurus*.

If the systematic position of *Callawayia* as a parvipelvian ichthyosaur holds true [235,236] and the new humerus is indeed assignable to this taxon, it would indicate that in addition to the more basal, non-ichthyosaurian ichthyopterygians, mixosaurids [241], and giant shastasaurids, also the more derived parvipelvian ichthyosaurs with thunniform (= tuna-like) body shapes were already present in the Early Triassic.

Triassic ichthyosaurs show a close correlation between humerus proximodistal length and overall body length of the animals (Fig. 3). Comparison of the new humerus (NMMNH P-65886) from Bear Lake County, Idaho, with the other Triassic ichthyosaurs such as *Cymbospondylus buchseri* Sander, 1989 from the Besano Formation, Monte San Giorgio, Switzerland [242], *C. piscosus* Leidy, 1868 from the Prida Formation, Nevada, USA [243,244], *Shonisaurus popularis* (Kosch, 1990) from the Late Triassic Luning Formation of Nevada, North America [245,246], and the shastasaurid *Guizhouichthyosaurus tangae* Cao & Luo in Yin *et al.*, 2000 from the Late Triassic of China ([13,247], the same specimen YIGMR TR00001 was figured as “*Panjiangsaurus epicharis*” in [248]; another specimen referred to as “*Shastasaurus*” *tangae* [IVPP V 11853]: [249]), indicated that NMMNH P-65886 did belong to an animal of about 11 meters in length (Fig. 3, Table S3 in File S1).

Another giant form, *Himalayasaurus tibetensis* Dong, 1972 from the Norian (Late Triassic) of Tibet, China, estimated to be about 15 meters in length [250,251] could not be added to the analysis, because it lacks a humerus for comparison. Instead, if *Temnodontosaurus trigonodon* (Theodori, 1854), a giant species from the Lower Jurassic of Europe that may have exceeded nine meters or more in total body length [120,252,253] is considered, it would provide further support for the validity of our size estimation, since it falls close to the regression line of the documented Triassic data ([252] presented data on specimen SMNS 15950: 786 cm body length, ca. 21.5 cm humerus length [morphotype 3]; data not included in Fig. 3 because only Triassic taxa are shown).

With regard to very large ichthyosaurs such as *Shastasaurus liangae* (see Yin in [247]) from the Late Triassic of southwestern China and *S. sikanniensis* from British Columbia, suction feeding has been proposed as a possible mode of feeding similar to that of modern tooth-less whales, i.e., the baleen whales or ziphiid beaked whales [234,235]. A recent comparative and biomechanical study of hyoid apparatuses and snout forms in Triassic and Early Jurassic ichthyosaurs, however, argues against this possibility,

instead indicating that all proposed “suction-feeders” are actually typical “ram-feeders” [254]. It is not known, whether the new Spathian ichthyosaur humerus from Bear Lake County belonged to a true suction-feeding form or had a ram-feeding predatory lifestyle such as *Shonisaurus* or *Temnodontosaurus*. Independent of its ecology, the new specimen is important because it demonstrates that the Early Triassic ichthyosaur record is already quite diverse and that large ichthyosaurs, probably cruisers with higher metabolic rates that inhabited more open waters [255,256], which are more derived than the non-ichthyosaurian ichthyopterygians known from that time, were already widespread during the Spathian.

Hupehsuchia. *Nanchangosaurus suni* Wang, 1959 and *Hupehsuchus nanchangensis* Young & Dong, 1972, the two taxa currently included in Hupehsuchia Carroll & Dong, 1991, were either recovered from the Jialingjiang Formation or from the upper part of the Daye limestone of Hubei Province, China [198,257,258]. The age of these fossils is estimated to range from late Early Triassic [16,168,256,258,259] to early Middle Triassic [198,257,260]. Wu *et al.* [260] for example noted an estimated age of “about 242 million years” for *Nanchangosaurus*, which would correspond to the late Anisian, but these authors referred to it as Early Triassic in age. Li *et al.* [168] on the other hand, argued for an Early Triassic (Olenekian) age, indicating that *Nanchangosaurus* may actually be slightly older than *Hupehsuchus*. Nevertheless, accurate age dating of these fossils remains difficult [169]. Furthermore, the reader should be aware that accurate age dating of these fossils is currently equivocal, depending on the definition of the Olenekian-Anisian boundary [36]. Similarly, very little is known about the dietary preferences of both taxa [257]. The systematic position of Hupehsuchia are presently not well understood, even though *Hupehsuchus* was recovered as sister taxon to Ichthyopterygia before [130].

Discussion

Our results show that the prolonged step-wise recovery pattern of marine ecosystems following the end-Permian mass extinction as recently presented ([20]: Fig. 4) is incorrect and is in need of reconsideration as it does not reflect the global pattern. Outside China, there is ample evidence for large chondrichthyans and bony fishes as well as unusual marine temnospondyls shortly after the mass extinction, suggesting an early radiation of marine predators. Measurements of fishes show that the median body length significantly decreased from around 20 cm during the Early Triassic to about 15 cm in the Anisian (Mann-Whitney U test, $p < 0.01$). The overall range of fish body sizes remained similar but the distribution of body length also significantly decreased (Kolmogorov-Smirnov test, $p < 0.01$) between the Early Triassic and Anisian (Fig. 1). This reduction in body size is mainly the result of the diversification of small actinopterygian taxa (“subholosteans” and neopterygians) [52]. Fluctuations in fish body size distribution are observed at the sub-stage level during the Early Triassic, which may be due to lower sample size and differences in geographic sampling (Fig. 1). Marine tetrapods on the other hand show a non-significant (Mann-Whitney U and Kolmogorov-Smirnov tests) increase in body size between the Early Triassic and the Anisian (Fig. 1).

The fossil record clearly documents that already in Griesbachian and Dienerian times (Induan, earliest Triassic, Fig. 4A), global marine ecosystems did not consist of primary producers exclusively ([20]: p. 380, Fig. 3), but rather exhibited several trophic levels up to and including the presence of large aquatic vertebrates such as predatory bony fishes (e.g., *Saurichthys*, *Birgeria*,

Rebellatrix, Fig. 4), chondrichthyans (e.g. *Hybodus*, Eugeneodontiformes, Fig. 4) and marine temnospondyl ‘amphibians’, such as the gharial-like lonchorhynchine trematosauroids with elongated slender snouts (e.g., *Aphaneramma*, *Wantzosaurus*, Fig. 4); faunal elements that would fall in the category P₂ (“predatory fishes and reptiles”) of the trophic pyramid depicted in [20] (p. 379, Fig. 2). Although the marine temnospondyls are not specifically listed in the definition of category P₂, these animals nevertheless still preyed upon smaller organisms of levels P₁ (“predatory invertebrates”) and P₂, analogous to the larger predatory reptiles [20]. None of the Early Triassic species of marine trematosauroid temnospondyls are dominant over other taxa and they can therefore not represent “disaster taxa” (*sensu* [261]). The group ranged from the temperate zone in the North (Greenland and Spitsbergen, which were not in the polar region as they are today) to the temperate zone in the South (e.g., Madagascar) and must thus be considered supra-regionally to even globally distributed in the Early Triassic. Following Kauffmann and Harries ([261]: p. 21), the marine temnospondyls are instead interpreted herein as “crisis progenitors”, which “initially adapted to perturbed environmental conditions of the mass extinction interval, readily survive this interval, and are among the first groups to seed subsequent radiation into unoccupied ecospace during the survival and recovery intervals”. The same applies for fishes: Although there are many cosmopolitan genera during the Early Triassic [56,59,91], the taxonomic composition of the faunas is well-balanced, with no taxon predominating in terms of fossil abundance [102].

In order for a diversity of large marine predators to exist in the Early Triassic, at least a minimum interaction between primary producers, primary and secondary consumers (e.g., smaller fishes, conodonts, ammonoids) as well as the higher levels in the food web is essential, because these animals could not have thrived on the broader but lower trophic levels alone. This reasoning is supported by the body size survey of fishes in the Early Triassic and Anisian, which, if taken as proxies for trophic level [67], clearly support the existence of a multilevel trophic pyramid from the Griesbachian onwards. Thus, there is no basis for the claim ([20]: p. 379–380) that “[...] ecosystems were constructed step by step from low to top trophic levels through Early–Middle Triassic times [...]”.

The recent publications addressing the recovery of marine trophic networks following the end-Permian event [11,20] are further biased by the focus on conditions in China only rather than on a global perspective, and thus they do not fully represent the current state of research. This is for the most part due to the omission of fossil data and older literature, especially concerning groups not (yet) known in China, which has fundamental effects on the timing of recovery of the food chains after the end-Permian mass extinction. Equally important data from non-Chinese Early Triassic localities (e.g., Svalbard, Madagascar, Greenland, western Canada) that may contradict their presented delayed recovery patterns are less prominently discussed. Such data sets, especially pertaining to larger marine vertebrates [59] [121,154], must be included into the discussion regarding biotic recovery patterns. Additional to theoretical modeling, research on coprolites (see below) and gut contents, Ca-isotope analyses and functional studies on feeding mechanics (e.g., geometric morphometric and finite element analyses, tooth wear analyses) would help to better understand the role of the different predatory guilds in Early Triassic food webs, but such data are currently not readily available in the literature. However, a delayed recovery of higher trophic levels within oceanic food webs following the end-Permian mass extinction can already be refuted based on the known fossil record of marine predatory vertebrates.

Direct and Indirect Evidence for Predation

In addition to the direct evidence from the fossil record, indirect evidence is accumulating that suggests secondary marine reptiles likely evolved during the earlier stages of the Early Triassic. This is inferred from the high degree of adaptation to the aquatic environment, which is already present in the earliest known members of several of these independent marine reptilian lineages [121,222]. If we consider the well-studied mammalian examples of sirenian and cetacean evolution during the early Cenozoic as analogues, a time span of 5 to 10 million years could be plausible for a transition from predominantly terrestrial animals to fully aquatic forms with streamlined body shapes and paddle-like limbs [262,263]. Among Cetacea, the group including modern whales and dolphins, the transition from terrestrial (= land-living) *Pakicetus* Gingerich & Russell, 1981 (Early Eocene) to the first marine whales such as *Rodhocetus* Gingerich, Raza, Arif, Anwar & Zhou, 1994 or *Georgiacetus* Hulbert, Petkewich, Bishop, Bukry & Aleshire, 1998 (late Middle Eocene) required only about 5 million years [263–266]. Sirenia (sea cows), the only other extant group of fully aquatic mammals, began a similar transition from predominantly terrestrial to fully aquatic forms. *Prorastomus* Owen, 1855 (late Early and early Middle Eocene [267]) and *Pezosiren* Domning, 2001 (early Middle Eocene [268]) maintained semi-aquatic lifestyles. Fully aquatic forms such as *Protosiren* Abel, 1904 (Middle Eocene) retained hind limbs, even though they were probably no longer suited for terrestrial locomotion, whereas those of the extant dugongs and manatees eventually became completely reduced (as in whales, remnants of pelvic bones are still present; [262]).

If higher evolutionary rates are invoked for the Mesozoic marine reptiles, this would pointedly reduce the time span inferred for similar adaptations among the reptiles during the Early Triassic, however, one still has to expect these diverse lineages to be present shortly after the Permian-Triassic boundary, even though body fossils are not yet known from layers of earliest Triassic age. This is especially true for more derived early Spathian ichthyosaurs that, in addition to already having evolved large, streamlined bodies over 10 meters in total length (Fig. 3) and highly modified flipper morphologies only 2 myrs after the end-Permian extinction event [33,269], would also have experienced profound physiological and developmental adaptations (indicated in Fig. 4B by tail of large ichthyosaur, no. 15, reaching into the left-hand side of image). One such change, namely the reproductive modification from oviparity to viviparity (or ovoviviparity), would certainly have to be obligatory in this lineage [259,270]. It cannot be ruled out however that (ovo-)viviparity might have been already present in the terrestrial ancestors of the ichthyosaurs.

Another important source of information regarding predation is presented by phosphatic coprolites, some of which preserve fish remains (Fig. 2I–K; [271,272]). Some Early Triassic specimens from marine deposits measure nearly 10 cm in length [135]. Obviously, such coprolites derive from large predatory aquatic vertebrates, and based on body fossils of similar stratigraphic age, the most likely producers are large fishes such as *Birgeria*, *Saurichthys* or coelacanth, temnospondyl ‘amphibians’ or marine reptiles.

Sampling in the Early Triassic

According to the review-article of Chen & Benton [20], the authors do not consider the possibility that their “delayed recovery patterns” hypothesis following the end-Permian event could have been the result of sampling biases in Early Triassic sediments. With regard to larger marine vertebrates, we argue that biodiversity in the Early Triassic is underestimated for several reasons.

First of all, many marine reptilian lineages go through a shallow water phase before becoming fully pelagic [273]. Relatively smaller orbital and scleral ring diameters [259], as well as the apparent absence of bone collapse structures attributable to decompression syndrome corroborate the hypothesis that Triassic ichthyosaurs mainly inhabited shallow waters [274]. This is corroborated by the results of Cuthbertson *et al.* ([199]: p. 846) who, while discussing the yet elusive center of origin and early radiation of ichthyopterygians and presenting several possible pre-Olenekian dispersal routes, currently favour migration and dispersal “through shallow water regions between breaches in the otherwise continuous and contiguous continental landmasses”. Sections consisting of pelagic sediments, on the other hand, are usually studied more thoroughly because they often contain biostratigraphically important invertebrate fossils such as ammonoids, but they may not necessarily be the most likely sediments for preservation of these early forms of marine reptiles. Furthermore, the fossilization potential of marine vertebrates in sediments derived from near-shore environments will likely be reduced due to mechanical separation and disarticulation by wave action or scavenging.

Secondly, numerous sections that are known to contain Early Triassic marine vertebrates (or may potentially yield them) are restricted to remote areas (e.g., in polar regions such as Greenland and Spitsbergen) and thus are not as heavily sampled as other, more easily accessible areas. On the other hand, many classical, easily accessible, European Middle Triassic localities for marine vertebrates have been extensively researched for more than 150 years (e.g. Monte San Giorgio in southern Switzerland, German Muschelkalk Sea). Furthermore, many Early Triassic vertebrate fossils such as bony fishes are recovered from early diagenetic limestone nodules, which are restricted in size. Because of a lack of diagnostic characters, larger, incomplete specimens can often be determined only to higher taxonomic levels, thus distorting the actual diversity patterns.

Thirdly, locations yielding Early Triassic vertebrate fossils are still being recovered. Although the presence of Triassic marine reptiles from China has been known since the 1950s [275], it has only been during the last two decades that the global importance of the various reptile-bearing Triassic black shales of southern and southwestern China has been recognized [11,13,16,276]. Even though marine Triassic fishes from China have been described sporadically during the last century [277–279], they have experienced increased attention by researchers over the last decade [60,63,64,103,104,280–282]. Indeed, the fact that the Middle Triassic Luoping biota [18] was only recently discovered, well demonstrates that such ‘sampling biases’ in the fossil record can persist for a long time. Since its discovery, the extensive large-scale quarrying of the fossiliferous layers at the Luoping site has led to an amazing amount of fossil specimens (nearly 20000 recovered macrofossils in 2011 but most are yet to be described [11,18]), whereas sampling in other difficult to reach but potentially rewarding places such as Spitsbergen or Greenland is based mainly on sporadic, very expensive expeditions, where conditions generally allow for surface collecting only.

Fourthly, possibilities remain that Permian taxa might be recovered from Early Triassic sediments as well. For instance, in the 1920s, a diverse reptile fauna was reported from the Upper Permian Lower Sakamena Formation of Madagascar [283–285] that included procolophonoid and tangasaurid “younginiform” diapsids. Recently, however, new fossils typical of these predominantly Paleozoic reptiles were described from Early Triassic sediments (Middle Sakamena Formation), either from the “Couches à *Claraia* et Poissons” or “Couches à Poissons et

Ammonites” horizon, Diego Basin, northwestern Madagascar [286], which correspond to the local Otoceran (≈ Griesbachian) or Gyronian (≈ Dienerian) age, respectively [287]. If this age assignment holds true, the presence of the near-shore marine *Hovasauros boulei* Piveteau, 1926 ([284,285], see Fig. 4) as a potential survivor of the end-Permian mass extinction event is important for the present discussion. As a small-bodied reptile well-adapted to the aquatic environment (e.g., stomach stones as bone ballast; well-developed elongated swimming tail; pachyostotic ribs; [283,284]), it can be viewed as an Early Triassic analogue in terms of anatomy and ecology to the abundant pachypleurosaurid sauropterygians, which diversified later during the Triassic. These new discoveries therefore would yet increase the diversity of taxa present in the earliest Early Triassic food web. Another example of this kind would be the recent discovery of the typically Paleozoic chondrichthyan *Listracanthus* in the Early Triassic of Canada [84].

Finally, due to their position in the trophic web, apex predators are usually much rarer than primary and secondary consumers in the fossil record. If the remains of apex predators are, however, recovered in relatively large numbers, as is for example the case for ichthyosaurs and trematosauroids from the Early Triassic of Spitsbergen, Greenland and Madagascar [120,135,144,152,191], this argues against a truncation of the higher trophic levels.

The Predators’ Influence on Ecosystems

Where present in the Early Triassic, a disturbed “evenness” with dominance of individual species over others (see above) is not recognized among marine fishes or the larger marine tetrapod lineages. Instead it appears that many of the novel “numerous predatory levels” proposed for the Luoping biota [20] were already present during the Early Triassic (Table 1). This categorization scheme is not interpreted as being exclusive, but instead, is indicative of trophic feeding preferences. It thus becomes apparent that even in the early stages of the Early Triassic, longer food chains than those previously proposed [20] must have been present, which argues against a delayed recovery of the upper levels within marine food webs after the end-Permian mass extinction.

The omission of the large marine temnospondyls, and the neglect of the global Early Triassic record of large predatory fishes in the discussion concerning the reconstruction of marine food chains and the associated timing of the recovery following the end-Permian event erroneously led to the conclusion [20] that higher trophic levels were absent until Middle Triassic times. The widespread presence of large marine predators indicates that numerous prey such as small fishes, conodonts, crustaceans and molluscs (primary and secondary consumers) must have been abundant in the Early Triassic, suggesting that multi-level trophic networks were already established shortly after the end-Permian event, although the taxonomic composition was different from that prior to the mass extinction. Furthermore, the larvae and juveniles of predatory fishes probably fed on different prey items than adult individuals (e.g. eggs and larvae of other animals, ostracods), thus presumably adding more complexity to the trophic network. If juvenile trematosauroids were not exclusively piscivorous, but instead, were opportunistic feeders preying upon a variety of smaller animals including invertebrates (Table 1), this would add yet another level of predator-prey interaction to the system. It is noteworthy that despite their abundance elsewhere in the Early Triassic, trematosauroid temnospondyls have yet to be discovered in sediments of that age in China [122,154].

Early Triassic ecosystems excluding those of China contain an array of predatory organisms (see above, Fig. 4). The conclusion

Table 1. Predator-prey relationships during the Early Triassic.

	durophagous predators	Small and mid-sized carnivores	larger carnivores
Prey items:	Invertebrates (e.g., cephalopods, gastropods, bivalves, crustaceans)	Invertebrates	Invertebrates
		conodonts?	conodonts?
		fishes	fishes
			smaller carnivores (e.g., juvenile trematosauroids and reptiles)
Vertebrate predators:	chondrichthyan fishes	chondrichthyan fishes	chondrichthyan fishes
	<i>Acrodus, Palaeobates</i>	<i>Hybodus</i>	<i>Hybodus, Eugeneodontiformes</i>
	actinopterygian fishes	actinopterygian fishes	actinopterygian fishes
	<i>Bobasatrania</i>	<i>Birgeria, Saurichthys</i>	<i>Birgeria, Saurichthys</i>
	actinistian fishes	actinistian fishes	ichthyosaurs
	<i>Myliacanthus, Scleracanthus</i>	<i>Rebellatrix</i>	<i>Pessopteryx, Quasianosteosaurus, ?Callawayia</i> -like ichthyosaurs
	ichthyosaurs	thalattosaurs	temnospondyl ‘amphibians’
	<i>Omphalosaurus, Chaohusaurus</i>	<i>Paralonectes, Agkistrognathus</i>	<i>Svalbardosaurus</i>
		trematosauroid ‘amphibians’	
		<i>Aphaneramma, Wantzosaurus</i>	
		sauropterygians	
		<i>Corosaurus, ?Kwangsisaurus</i>	
		ichthyosaurs	
		<i>Utatusaurus, Grippia</i>	
		hupehsuchians?	
		<i>Hupehsuchus, Nanchangosaurus</i>	

Only a few examples are given for each group. Note that even though conodonts are not listed specifically, they nevertheless would have contributed to the ancient food webs as both predators and prey. See text for references.

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that marine ecosystems immediately following the PT-mass extinction “[...] were degraded to a low level, typified by primary producers or opportunistic consumers [...]” ([20]; p. 379) lacks global support, and could perhaps be a peculiarity of the Chinese fossil record, in the worst of all cases. As is clearly evident in the fossil record, the marine trophic pyramid was not truncated in the Early Triassic. The presence of multiple trophic levels at the onset of the Triassic (Griesbachian) is supported by the variety of shapes and body sizes of marine predators, as well as their global distribution and abundance in the fossil record. After the loss of the dominant Paleozoic marine apex predators (mainly chondrichthyans, e.g., [20,24,26,52]) during the PT mass extinction, the higher levels of the trophic pyramid were rapidly occupied by other vertebrate groups, first mainly by temnospondyl ‘amphibians’ and fishes and later predominantly by marine reptiles and fishes (Fig. 4). The appearance of secondary marine reptiles as apex predators in the Triassic cannot be used as a metric for the timing of biotic recovery [20], since, as stated by the authors, these groups were not among the dominant apex predators in the ocean before the mass extinction event. Secondary marine reptiles instead should be regarded as an evolutionary novelty, just as the marine trematosauroid ‘amphibians’ that appeared earlier. Although taxonomic richness of marine vertebrates continued to rise from the Early to the Middle Triassic (e.g., [26–28,117,124]), and hence the complexity of trophic networks probably increased likewise, we emphasize that the diversity among Early Triassic apex predators as well as their prey already allowed for a variety of trophic interactions and food chains of usual lengths.

The Smithian-Spathian Turnover of Apex Predators

The emergence of some of the dominant marine reptiles of the Mesozoic, i.e. ichthyopterygians and sauropterygians, as apex predators in the Spathian roughly coincides with the disappearance of marine temnospondyl ‘amphibians’ and eugeneodontiform sharks. Marine temnospondyls are predominantly known from the Griesbachian, Dienerian and Smithian sub-stages of the Early Triassic [122,154,288], where they had a global distribution (Fig. 4, Table S2 in File S1), although there is indication that an Anisian trematosauroid from Jordan might have inhabited also shallow marine coastal regions [289]. Early Triassic eugeneodontiform remains, where well-dated, are usually from horizons older than the Spathian [78,79,82]. This turnover among marine apex predators falls within the Smithian-Spathian transition (Fig. 4), which is well-known for the major near-extinction of nekto-pelagic clades such as ammonoids and conodonts (e.g., [50,290,291]). The Smithian-Spathian boundary crisis was linked with a profound climatic change from warmer and more humid conditions during the Smithian to cooler and dryer conditions in the Spathian ([4] and references therein). The processes by which the Smithian-Spathian-boundary event [292], approximately 2 myr after the main extinction pulse near the Permian-Triassic boundary, modulated the Early Triassic apex predator turnover remains to be explored.

A similar turnover scenario may have been linked to the end-Permian mass extinction when the dominant marine predators of the Late Paleozoic (mainly fishes) were replaced by trematosauroid and other temnospondyl ‘amphibians’, as well as by new taxa of

predatory osteichthyans (*Birgeria*, *Saurichthys*, *Rebellatrix*). If we examine the continental vertebrate record in the world-famous Karoo section in southern Africa for comparison, we note that the end-Permian extinction event appeared to be selective in that certain tetrapod lineages suffered more than others; whereas the decrease in overall generic diversity of terrestrial vertebrates is related mainly to the severe decline in synapsid diversity and also to a small degree to the decline of fish generic richness, the diversity of 'amphibians' and reptiles actually increases across the Permian-Triassic boundary ([26], [5]: Fig. 1A). This increase in diversity of both groups may have supported the colonization of near-shore environments during the Early Triassic, first by the temnospondyl 'amphibians' and some two millions years later by secondary marine reptiles.

Conclusions

- (1) Global fossil evidence clearly demonstrates that marine apex predators were always present during the earliest Triassic (from the Griesbachian onward), thus emphasizing the regeneration and/or inheritance of full length, multi-level trophic food webs immediately after the end-Permian mass extinction.
- (2) Spatial and stratigraphic distribution of marine predatory vertebrates (fishes, temnospondyl 'amphibians', and reptiles) does not support a step-wise recovery model of Triassic trophic webs.
- (3) A sharp faunal turnover among marine predatory guilds during the Early Triassic is apparent and was centered around the Smithian-Spathian boundary, because those ecosystems with predominantly trematosauroid temnospondyl 'amphibians' and fishes as apex predators switched to ecosystems with marine reptiles (ichthyosaurs, sauropterygians, thalattosaurs, protorosaurians) and fishes at the uppermost end of the food chain.
- (4) The disturbance of ecosystems during and after the Permian-Triassic mass extinction event may have triggered the evolution and early diversification of marine vertebrate groups such as actinopterygian fishes, as well as secondary marine temnospondyl 'amphibians'.
- (5) There is no significant increase in body size of marine apex predators (fishes, tetrapods) from the Early Triassic to the Anisian (early Middle Triassic), invalidating previous assumptions of a step-wise recovery of the trophic pyramid after the end-Permian event.

Supporting Information

File S1 Table S1. Xcel-spreadsheet with maximum standard lengths of marine species of bony fishes (Actinistia, Actinopterygii) in the Early Triassic and the Anisian (Middle Triassic) based on literature data. Table S2. Xcel-spreadsheet with list of tetrapod species surveyed and accompanying occurrence and maximum size (= total length) data. The compilation of Middle Triassic taxa is based on Kelley *et al.* (2012) [124] with some taxa, reference and size data modified or added. Table S3. Xcel-spreadsheet with data used for the humeral proximodistal length-body length relation in Triassic ichthyosaurs (Fig. 3). (XLSX)

File S2 Additional references accompanying Tables S1–S2 in File S1. (DOC)

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Author Contributions

Conceived and designed the experiments: TMS CR HB. Analyzed the data: TMS CR JJ HB. Contributed reagents/materials/analysis tools: CR JJ HB. Wrote the paper: TMS CR. Checked and improved the last draft version of the manuscript: TMS CR JJ HB.

References

- Payne JL, Clapham ME (2012) End-Permian mass extinction in the oceans: an ancient analog for the twenty-first century? *Annu Rev Earth Planet Sci* 40: 89–111 [doi: 10.1146/annurev-earth-042711-105329].
- Benton MJ, Tverdokhlebov VP, Surkov MV (2004) Ecosystem remodelling among vertebrates at the Permian-Triassic boundary in Russia. *Nature* 432: 97–100 [doi: 10.1038/nature02950].
- Jackson JBC, Erwin DH (2006) What can we learn about ecology and evolution from the fossil record? *Trends Ecol Evol* 21: 322–328 [doi:10.1016/j.tree.2006.1003.1017].
- Romano C, Goudemand N, Vennemann TW, Ware D, Schneebeli-Hermann E, et al. (2013) Climatic and biotic upheavals following the end-Permian mass extinction. *Nature Geoscience* 6: 57–60 [doi: 10.1038/NGEO1667].
- Fröbisch J (2013) Vertebrate diversity across the end-Permian mass extinction — Separating biological and geological signals. *Palaeogeogr Palaeoclimatol Palaeoecol* 372: 50–61 [doi: 10.1016/j.palaeo.2012.1010.1036].
- Brühwiler T, Bucher H, Ware D, Schneebeli-Hermann E, Hochuli PA, et al. (2012) Smithian (Early Triassic) ammonoids from the Salt Range, Pakistan. *Spec Pap Palaeontol* No. 88: 1–114 [ISBN: 978-1-4443-6713-3].
- Casini M, Blenckner T, Möllmann C, Gärdmark A, Lindegren M, et al. (2012) Predator transitory spillover induces trophic cascades in ecological sinks. *Proc Natl Acad Sci USA* 109: 8185–8189 [doi: 10.1073/pnas.1113286109].
- Steneck RS (2012) Apex predators and trophic cascades in large marine ecosystems: Learning from serendipity [Commentary]. *Proc Natl Acad Sci USA* 109: 7953–7954 [doi: 7910.1073/pnas.1205591109].
- Shen SZ, Crowley JL, Wang Y, Bowring SA, Erwin DH, et al. (2011) Calibrating the end-Permian mass extinction. *Science* 334: 1367–1372 [doi: 1310.1126/science.1213454].
- Mundil R, Pálfi J, Renne PR, Brack P (2010) The Triassic timescale: new constraints and a review of geochronological data. In: Lucas SG, editor. *The Triassic Timescale Geological Society, London, Special Publications*, 334. pp. 41–60 [doi: 10.1144/SP1334.1143].
- Benton MJ, Zhang Q, Hu S, Chen Z-Q, Wen W, et al. (2013) Exceptional vertebrate biotas from the Triassic of China, and the expansion of marine ecosystems after the Permo-Triassic mass extinction. *Earth Sci Rev* 125: 199–243 [doi: 10.1016/j.earscirev.2013.1005.1014].
- Wang X-f, Chen X-h, Chen L-d, Xu G-h, Wang C-s, et al. (2003) The Guanling biota—a unique “Fossilagerstätte” in the world. *Geology in China* 30: 20–35 [in Chinese with English abstract].
- Wang X, Bachmann GH, Hagdorn H, Sander PM, Cuny G, et al. (2008) The Late Triassic black shales of the Guanling area, Guizhou Province, south-west China: a unique marine reptile and pelagic crinoid fossil lagerstätte. *Palaeontology* 51: 27–61 [doi: 10.1111/j.1475–4983.2007.00735.x].
- Motani R, Jiang D-Y, Tintori A, Sun Y-L, Hao W-C, et al. (2008) Horizons and assemblages of Middle Triassic marine reptiles from Panxian, Guizhou, China. *J Verteb Paleontol* 28: 900–903 [doi: 10.1671/0272-4634(2008)28[900:HAAOMT]2.0.CO;2].
- Jiang D, Motani R, Li C, Hao W, Sun Y, et al. (2005) Guanling Biota: a marker of Triassic biotic recovery from the end-Permian extinction in the ancient Guizhou Sea. *Acta Geologica Sinica* 79: 729–738 [doi: 10.1111/j.1755-6724.2005.tb00926.x].
- Li J-L (2006) A brief summary of the Triassic marine reptiles of China. *Vertebr Palasiat* 44: 99–108.
- Jiang D, Motani R, Hao W, Rieppel O, Sun Y, et al. (2009) Biodiversity and sequence of the Middle Triassic Panxian marine reptile fauna, Guizhou

- Province, China. *Acta Geologica Sinica* 83: 451–459 [doi: 10.1111/j.1755-6724.2009.00047.x].
18. Hu S-x, Zhang Q-y, Chen Z-q, Zhou C-y, Lü T, et al. (2011) The Luoping biota: exceptional preservation, and new evidence on the Triassic recovery from end-Permian mass extinction. *Proc R Soc B* 278: 2274–2282 [doi: 10.1098/rspb.2010.2235].
 19. Zhang QY, Zhou CY, Lü T, Xie T, Lou XY, et al. (2008) Discovery and significance of the Middle Triassic Anisian biota from Luoping, Yunnan Province [in Chinese]. *Geological Review* 54: 145–149.
 20. Chen Z-Q, Benton MJ (2012) The timing and pattern of biotic recovery following the end-Permian mass extinction. *Nature Geoscience* 5: 375–383 [doi: 10.1038/Ngeo1475].
 21. Erwin DH (1998) The end and the beginning: recoveries from mass extinctions. *Trends Ecol Evol* 13: 344–349.
 22. Payne JL, Lehmann DJ, Wei J, Orchard MJ, Schrag DP, et al. (2004) Large perturbations of the carbon cycle during recovery from the End-Permian extinction. *Science* 305: 506–509 [doi: 10.1126/science.1097023].
 23. Camargo JA (1995) On measuring species evenness and other associated parameters of community structure. *Oikos* 74: 538–542.
 24. Koot MB (2013) Effects of the Late Permian mass extinction on chondrichthyan palaeobiodiversity and distribution patterns. PhD Thesis, Plymouth, UK: Plymouth University. 853 p.
 25. Benson RB, Butler RJ, Lindgren J, Smith AS (2010) Mesozoic marine tetrapod diversity: mass extinctions and temporal heterogeneity in geological megabiases affecting vertebrates. *Proc R Soc B* 277: 829–834 [doi: 10.1098/rspb.2009.1845].
 26. Pirat CW (1973) Vertebrates and the Permo-Triassic extinction. *Palaeogeogr Palaeoclimatol Palaeoecol* 14: 249–264.
 27. Thomson KS (1977) The pattern of diversification among fishes. In: Hallam A, editor. *Patterns of Evolution as Illustrated by the Fossil Record* [591 pp]. Amsterdam: Elsevier. pp. 377–404.
 28. Friedman M, Sallan LC (2012) Five hundred million years of extinction and recovery: a phanerozoic survey of large-scale diversity patterns in fishes. *Palaeontology* 55: 707–742 [doi: 10.1111/j.1475-4983.2012.01165.x].
 29. Roopnarine PD, Angielczyk KD, Wang SC, Hertog R (2007) Trophic network models explain instability of Early Triassic terrestrial communities. *Proceedings of the Royal Society, B* 274: 2077–2086 [doi: 10.1098/rspb.2007.0515].
 30. Tuomisto H (2010) A consistent terminology for quantifying species diversity? Yes, it does exist. *Oecologia* 164: 853–860 [doi:10.1007/s00442-00010-01812-00440].
 31. Brack P, Rieber H, Nicora A, Mundil R (2005) The Global boundary Stratotype section and Point (GSSP) of the Ladinian Stage (Middle Triassic) at Bagolino (Southern Alps, Northern Italy) and its implications for the Triassic time scale. *Episodes* 28: 233–244.
 32. Furin S, Preto N, Rigo M, Roghi G, Gianolla P, et al. (2006) High-precision U-Pb zircon age from the Triassic of Italy: Implications for the Triassic time scale and the Carnian origin of calcareous nannoplankton and dinosaurs. *Geology* 34: 1009–1012.
 33. Ovtcharova M, Bucher H, Schaltegger U, Galfetti T, Brayard A, et al. (2006) New Early to Middle Triassic U-Pb ages from South China: Calibration with ammonoid biochronozones and implications for the timing of the Triassic biotic recovery. *Earth and Planetary Science Letters* 243: 463–475 [doi:10.1016/j.epsl.2006.1001.1042].
 34. Galfetti T, Bucher H, Ovtcharova M, Schaltegger U, Brayard A, et al. (2007) Timing of the Early Triassic carbon cycle perturbations inferred from new U-Pb ages and ammonoid biochronozones. *Earth and Planetary Science Letters* 258: 593–604 [doi:10.1016/j.epsl.2007.1004.1023].
 35. Gradstein FM, Ogg JG (2004) *Geological Time Scale 2004 - Why, how, and where next!* Lethaia 37: 175–181 [doi: 10.1080/00241160410006483].
 36. Goudemand N, Orchard MJ, Bucher H, Jenks J (2012) The elusive origin of *Chiosella timorensis* (Conodont Triassic). *Geobios* 45: 199–207 [doi:10.1016/j.geobios.2011.1006.1001].
 37. Zhang Y, Zhan K-X, Shi GR, He W-H, Yuan D-X, et al. (2014) Restudy of conodont biostratigraphy of the Permian-Triassic boundary section in Zhongzhai, southwestern Guizhou Province, South China. *Journal of Asian Earth Sciences* 80: 75–83 [doi: 10.1016/j.jseaes.2013.1010.1032].
 38. Guex J, Hungerbühler A, Jenks J, O'Dogherty L, Atudorei V, et al. (2010) Spathian (Lower Triassic) ammonoids from western USA (Idaho, California, Utah and Nevada). *Mémoires de Géologie (Lausanne)* 49: 1–92.
 39. Griffith J (1959) On the anatomy of two saurichthyid fishes, *Saurichthys striolatus* (Bronn) and *S. curioni* (Bellotti). *Proceedings of the Zoological Society of London* 132: 587–606 [doi: 10.1111/j.1469-7998.1959.tb05538.x].
 40. Rieppel O (1992) A new species of the genus *Saurichthys* (Pisces: Actinopterygii) from the Middle Triassic of Monte San Giorgio (Switzerland), with comments on the phylogenetic interrelationships of the genus. *Palaeontographica Abt A* 221: 63–94.
 41. Nielsen E (1949) Studies on Triassic fishes from East Greenland 2. *Australosomus* and *Birgeria*. *Palaeozoologica Groenlandica* 3: 1–309.
 42. Romano C, Brinkmann W (2009) Reappraisal of the lower actinopterygian *Birgeria steniosaei* ALDINGER, 1931 (Osteichthyes; Birgeriidae) from the Middle Triassic of Monte San Giorgio (Switzerland) and Besano (Italy). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 252: 17–31 [doi: 10.1127/0077-7749/2009/0252-0017].
 43. Schindelin J, Arganda-Carreras I, Frise E, Kaynig V, Longair M, et al. (2012) Fiji: an open-source platform for biological-image analysis. *Nature Methods* 9: 676–682 [doi: 10.1038/nmeth.2019].
 44. Hammer Ø, Harper DAT, Ryan PD (2001) *Paleontological statistics software package for education and data analysis*. *Palaeontologia Electronica* 4: 9pp., 178 kb [http://palaeo-electronica.org/2001_1/past/issue1_01.htm].
 45. Kuraku S, Kuratani S (2006) Time scale for cyclostome evolution inferred with a phylogenetic diagnosis of hagfish and lamprey cDNA sequences. *Zoological Science* 23: 1053–1064 [doi: 10.2108/zsj.23.1053].
 46. Goudemand N, Orchard MJ, Li G, Urdy S, Bucher H, et al. (2011) Synchrotron-aided reconstruction of the conodont feeding apparatus and implications for the mouth of the first vertebrates. *Proc Natl Acad Sci USA* 108: 8720–8724 [doi: 10.1073/pnas.1101754108].
 47. Goudemand N, Orchard MJ, Tafforeau P, Urdy S, Brühwiler T, et al. (2012) Early Triassic conodont clusters from South China: revision of the architecture of the 15 element apparatuses of the superfamily Gondolelloidea. *Palaeontology* 55: 1021–1034 [doi: 10.1111/j.1475-4983.2012.01174.x].
 48. Turner S, Burrow CJ, Schultze H-P, Bieck A, Reif W-E, et al. (2010) False teeth: conodont-vertebrate phylogenetic relationships revisited. *Geodiversitas* 32: 545–594 [doi: 10.5252/g2010n5254a5251].
 49. Janvier P (2008) Homologies and evolutionary transitions in early vertebrate history. In: Anderson JS, Sues H-D, editors. *Major Transitions in Vertebrate Evolution*. Bloomington: Indiana University Press. pp. 57–121.
 50. Orchard MJ (2007) Conodont diversity and evolution through the latest Permian and Early Triassic upheavals. *Palaeogeogr Palaeoclimatol Palaeoecol* 252: 93–117 [doi: 10.1016/j.palaeo.2006.1011.1037].
 51. Tintori A, Hitiš T, Jiang D-Y, Lombardo C, Sun Z-Y (2013) Triassic actinopterygian fishes: the recovery after the end-Permian crisis. *Integrative Zoology* [doi: 10.1111/1749-4877.12077].
 52. Romano C, Koot MB (2013) Evolutionary dynamics of fishes through the Late Permian mass extinction. 125th Anniversary Annual Meeting of the Geological Society of America, 27–30 October, 2013, Denver, Colorado, USA.
 53. Guinot G, Adnet S, Capetta H (2012) An analytical approach for estimating fossil record and diversification events in sharks, skates and rays. *PLoS ONE* 7(9): e44632, [doi: 10.1371/journal.pone.0044632].
 54. Guinot G, Adnet S, Cavin L, Capetta H (2013) Cretaceous stem chondrichthyans survived the end-Permian mass extinction. *Nat Commun* 4:2669, [doi:10.1038/ncomms3669].
 55. Lehman J-P (1952) Etude complémentaire des poissons de l'Eotrias de Madagascar. *K Sven Vetenskapsakad Handl* 4: 1–192.
 56. Schaeffer B, Mangus M (1976) An Early Triassic fish assemblage from British Columbia. *AMNH Bull* 156: 515–564.
 57. Stensjö E (1932) Triassic fishes from East Greenland 1–2. *Medd Gronl* 83: 1–298.
 58. Stensjö E (1921) Triassic Fishes from Spitzbergen 1. Vienna: Adolf Holzhausen. 307 p.
 59. Brinkmann W, Romano C, Bucher H, Ware D, Jenks J (2010) Palaeobiogeography and stratigraphy of advanced gnathostomian fishes (Chondrichthyes and Osteichthyes) in the Early Triassic and from selected Anisian localities (Report 1863–2009). *Zbl Geol Paläont, Teil II* 2009: 765–812.
 60. Li Q (2009) A new parasemionotid-like fish from the Lower Triassic of Jurong, Jiangsu Province, South China. *Palaeontology* 52: 369–384 [doi: 10.1111/j.1475-4983.2009.00848.x].
 61. Tong J, Zhao L (2011) Lower Triassic and Induan-Olenekian Boundary in Chaohu, Anhui Province, South China. *Acta Geologica Sinica* 85: 399–407 [doi: 10.1111/j.1755-6724.2011.00408.x].
 62. Jin F (2006) An overview of Triassic fishes from China. *Vertebr Palasiat* 44: 28–42.
 63. Liu G-B, Feng H-Z, Wang J-X, Wu T-M, Zhai Z-H (2002) Early Triassic fishes from Jurong, Jiangsu [in Chinese with English summary]. *Acta Palaeontol Sin* 41: 27–52.
 64. Tong J, Zhou X, Erwin DH, Zuo J, Zhao L (2006) Fossil fishes from the Lower Triassic of Majiashan, Chaohu, Anhui Province, China. *J Paleontol* 80: 146–161 [doi: 10.1666/0022-3360(2006)080[0146:FFFTLT]2.0.CO;2].
 65. Wang NZ, Yang SR, Jin F, Wang W (2001) Early Triassic Hybodontidae from Tiandong of Guangxi, China. First report on the fish sequence study near the Permian-Triassic boundary in South China [in Chinese with English Abstract]. *Vertebr Palasiat* 39: 237–250.
 66. Zhao L-J, Lu L-W (2007) A new genus of Early Triassic perleidid fish from Changxing, Zhejiang, China [in Chinese with English summary]. *Acta Palaeontol Sin* 46: 238–243.
 67. Romanuk TN, Hayward A, Hutchings JA (2011) Trophic level scales positively with body size in fishes. *Global Ecol Biogeogr* 20: 231–240 [doi: 10.1111/j.1466-8238.2010.00579.x].
 68. Trebilco R, Baum JK, Salomon AK, Dulvy NK (2013) Ecosystem ecology: size-based constraints on the pyramids of life. *Trends Ecol Evol* 28: 423–431 [doi: 10.1016/j.tree.2013.03.008].
 69. Błażejowski B (2004) Shark teeth from the Lower Triassic of Spitsbergen and their histology. *Polish Polar Research* 25: 153–167.
 70. Romano C, Brinkmann W (2010) A new specimen of the hybodont shark *Palaeobates polaris* with three-dimensionally preserved Meckel's cartilage from the Smithian (Early Triassic) of Spitsbergen. *J Vertebr Paleontol* 30: 1673–1683 [doi: 10.1080/02724634.2010.521962].

71. Mutter RJ, Neuman AG, de Blanger K (2008) *Homalodontus* nom. nov., a replacement name for *Wapitodus* Mutter, de Blanger and Neuman, 2007 (Homalodontidae nom. nov., Hybodontidae), preoccupied by *Wapitodus* Orchard, 2005. Zool J Linn Soc 154: 419–420 [doi: 10.1111/j.1096-3642.2008.00488.x].
72. Mutter RJ, de Blanger K, Neuman AG (2007) Elasmobranchs from the Lower Triassic Sulphur Mountain Formation near Wapiti Lake (BC, Canada). Zool J Linn Soc 149: 309–337 [doi: 10.1111/j.1096-3642.2007.00244.x].
73. Maisey JG (1989) *Hamiltonichthys mapei*, g. & sp. nov. (Chondrichthyes, Elasmobranchii), from the Upper Pennsylvanian of Kansas. Am Mus Novitates No. 2931: 1–34.
74. Ivanov A, Klets T (2007) Triassic marine fishes from Siberia, Russia. In: The Global Triassic (Lucas, S. G., Spielmann, J. A., eds.) NMMNH Sci Bull 41: 108–109.
75. Yamagishi H (2004) Elasmobranch remains from the Taho Limestone (Lower-Middle Triassic) of Ehime Prefecture, southwest Japan. In: Arratia G, Tintori A, editors. Mesozoic Fishes 3, Systematics, Palaeoenvironments and Biodiversity Proceedings of the International Meeting, Serpiano, 2001. Munich: Dr. Friedrich Pfeil. pp. 565–574.
76. Tapanila L, Pruit J, Pradel A, Wilga CD, Ramsay JB, et al. (2013) Jaws for a spiral-tooth whorl: CT images reveal novel adaptation and phylogeny in fossil *Helicoprion*. Biol Lett 9: 20130057. [doi: 10.1098/rsbl.2013.0057].
77. Ginter M, Hampe O, Duffin CJ (2010) Chondrichthyes. Paleozoic Elasmobranchii: Teeth. Handbook of Paleoichthyology, Volume 3D: 1–168.
78. Mutter RJ, Neuman AG (2008) New eugeneodontid sharks from the Lower Triassic Sulphur Mountain Formation of Western Canada. In: Cavin L, Longbottom A, Richter M, editors. Fishes and the Break-up of Pangaea. Geol Soc London Spec Publ 295: 9–41.
79. Birkenmajer K, Jerzmańska A (1979) Lower Triassic shark and other fish teeth from Hornsund, South Spitsbergen. In: Birkenmajer, K, editor. Results of the Polish Spitsbergen Expeditions, part 10. Stud Geol Pol 60: 7–38.
80. Nielsen E (1952) On new or little known Edestidae from the Permian and Triassic of East Greenland. Medd Grøn 144: 1–55.
81. Kasumzadeh AA (2000) Sostojani'e izuchennosti triasovykh otlozhenij Azerbaidzhana i problemy granizy permi i triasa [Advances in research of the Triassic deposits in Azerbaijan and problems of the Permian-Triassic boundary]. Baku: Nafta-Press. 116 p.
82. Obruchev DB (1965) Razviti'e i smena morskikh organizmov na rubezhe paleozoya i mezozoya [Development and change of marine organisms at the Palaeozoic-Mesozoic boundary] [in Russian]. Trudy Paleontologicheskii Institut 108: 266–267.
83. Zhang M-M (1976) A new species of helicoprionid shark from Xizang [in Chinese with English summary]. Scientia Geologica Sinica 1976: 332–336.
84. Mutter RJ, Neuman AG (2006) An enigmatic chondrichthyan with Paleozoic affinities from the Lower Triassic of western Canada. Acta Palaeontol Polon 51: 171–182.
85. Mutter RJ, Neuman AG (2009) Recovery from the end-Permian extinction event: Evidence from “Lilliput *Listracanthus*”. Palaeogeogr Palaeoclimatol Palaeoecol 284: 22–28 [doi: 10.1016/j.palaeo.2009.1008.1024].
86. Schultze H-P (2004) Mesozoic sarcopterygians. In: Arratia G, Tintori A, editors. Mesozoic fishes 3 Systematics, Palaeoenvironments and Biodiversity. München: Dr. Friedrich Pfeil. pp. 463–492.
87. Lehman J-P (1956) Compléments à l'étude des genres *Ecerinosomus* et *Bobasatrania* de l'Eotrias de Madagascar. Ann Pal 42: 67–94.
88. Russell LS (1951) *Bobasatrania? canadensis* (Lambe), a giant chondrosteian fish from the Rocky Mountains. Natl Mus Can Bull 123: 218–224.
89. Kogan I (2011) Remains of *Saurichthys* (Pisces, Actinopterygii) from the Early Triassic Wordie Creek Formation of East Greenland. Bull Geol Soc Den 59: 93–100.
90. Stensiö E (1925) Triassic fishes from Spitzbergen 2. K Sven Vetenskapsakad Handl 3: 1–261.
91. Piveteau J (1935) Ressemblances des faunes ichthyologiques du Groenland et du Spitzberg avec celle de Madagascar au Trias inférieur. CR Séances Soc Géol Fr 1935: 113–114.
92. Nielsen E (1942) Studies on Triassic fishes from East Greenland 1. *Glaucolepis* and *Boreosomus*. Palaeozoologica Groenlandica 1: 1–403.
93. Lombardo C, Tintori A (2005) Feeding specializations in Late Triassic fishes. Annali dell'Università degli Studi di Ferrara Muscologia Scientifica e Naturalistica volume speciale 2005: 25–32.
94. Beltan L, Janvier P, Monod O, Westphal F (1979) A new marine fish and placodont reptile fauna of Ladinian age from Southwestern Turkey. N Jb Geol Paläont Mh 5: 257–267.
95. Mutter RJ, Cartanya J, Basaraba SAU (2008) New evidence of *Saurichthys* from the Lower Triassic with an evaluation of early saurichthyid diversity. In: Arratia G, Schultze H-P, Wilson MVH, editors. Mesozoic Fishes 4 Homology and Phylogeny. München: Dr. Friedrich Pfeil. pp. 103–127.
96. Mutter RJ (2005) Re-assessment of the genus *Helmolepis* Stensiö 1932 (Actinopterygii: Platyisthiidae) and the evolution of platyisthiids in the Early-Middle Triassic. Eclogae Geol Helv 98: 271–280 [doi: 10.1007/s00015-005-1164-7].
97. Romano C, Kogan I, Jenks J, Jerjen I, Brinkmann W (2012) *Saurichthys* and other fossil fishes from the late Smithian (Early Triassic) of Bear Lake County (Idaho, USA), with a discussion of saurichthyid palaeogeography and evolution. Bulletin of Geosciences 87: 543–570 [doi: 10.3140/bull.geosci.1337].
98. Beltan L (1980) Eotrias du nord-ouest de Madagascar: étude de quelques poissons, dont un est en parturition. Ann Soc Geol Nord 99: 453–464.
99. Guffroy S (1956) Notes paléoichthyologiques. Bull Soc Geol Fr 6: 847–854.
100. Piveteau J (1944–1945) Paléontologie de Madagascar XXV. - Les poissons du Trias inférieur, la famille des Saurichthyidés. Ann Pal 31: 79–89.
101. Rieppel O (1980) Additional specimens of *Saurichthys madagascariensis* Piveteau, from the Eotrias of Madagascar. N Jb Geol Paläont Mh 1980(1): 43–51.
102. Nielsen E (1961) On the Eotriassic fish faunas of central east Greenland. In: Raasch GO, editor. Geology of the Arctic 1. Toronto: University of Toronto Press. pp. 255–257.
103. Wu F, Sun Y, Hao W, Jiang D, Xu G, et al. (2009) A new species of *Saurichthys* (Actinopterygii: Saurichthyidae) from Middle Triassic (Anisian) of Yunnan Province, China. Acta Geologica Sinica, English Edition 83: 440–450 [doi: 10.1111/j.1755-6724.2009.00056.x].
104. Wu F, Sun Y, Xu G, Hao W, Jiang D, et al. (2011) New saurichthyid actinopterygian fishes from the Anisian (Middle Triassic) of southwestern China. Acta Palaeontol Polon 56: 581–614.
105. Zhang QY, Zhou CY, Lü T, Bai JK (2010) Discovery of Middle Triassic *Saurichthys* in the Luoping area, Yunnan, China [in Chinese, with English abstract]. Geological Bulletin of China 29: 26–30.
106. Wendruff AJ, Wilson MVH (2013) New Early Triassic coelacanth in the family Laugidae (Sarcopterygii: Actinistia) from the Sulphur Mountain Formation near Wapiti Lake, British Columbia, Canada. Can J Earth Sci 50: 904–910 [doi: 10.1139/cjes-2013-0010].
107. Clément G (1999) The actinistian (Sarcopterygii) *Piveteauia madagascariensis* Lehman from the Lower Triassic of Northwestern Madagascar: a redescription on the basis of new material. J Vertebr Paleontol 19: 234–242.
108. Wendruff AJ, Wilson MVH (2012) A fork-tailed coelacanth, *Rebellatrix divaricera*, gen. et sp. nov. (Actinistia, Rebellatricidae, fam. nov.), from the Lower Triassic of Western Canada. J Vertebr Paleontol 32: 499–511 [doi: 10.1080/02724634.2012.657317].
109. Benton MJ (2005) Vertebrate Paleontology. 3rd Edition. Malden, Ma: Blackwell Publishing Ltd. 455 p.
110. Böhm W, Sander PM (2010) Amniota, Nabeltiere. In: Westheide W, Rieger R, editors. Spezielle Zoologie Teil 2: Wirbel- oder Schädeltiere 2 Auflage. Heidelberg: Spektrum Akademischer Verlag. pp. 360–364.
111. Fröbisch J (2008) Global taxonomic diversity of anomodonts (Tetrapoda, Therapsida) and the terrestrial rock record across the Permian-Triassic boundary. PLoS ONE 3(11): e3733. [doi:10.1371/journal.pone.0003733].
112. Huttenlocker AK, Sidor CA (2012) Taxonomic revision of therocephalians (Therapsida: Theriodontia) from the Lower Triassic of Antarctica. Am Mus Novitates No 3738: 1–19.
113. Müller J, Reisz RR (2005) Four well-constrained calibration points from the vertebrate fossil record for molecular clock estimates. BioEssays 27: 1069–1075 [doi: 10.1002/bies.20286].
114. Witzmann F, Schoch RR, Maisch MW (2007) A relict basal tetrapod from Germany: first evidence of a Triassic chroniosuchian outside Russia. Naturwissenschaften 95: 67–72 [doi: 10.1007/s00114-00007-00291-00116].
115. Ruta M, Cisneros JC, Liebrecht T, Tsuji LA, Müller J (2011) Amniotes through major biological crises: faunal turnover among parareptiles and the end-Permian mass extinction. Palaeontology 54: 1117–1137 [doi: 10.1111/j.1475-4983.2011.01051.x].
116. Bardet N (1994) Extinction events among Mesozoic marine reptiles. Hist Biol 7: 313–324.
117. Bardet N (1995) Evolution et extinction des reptiles marins au cours du Mésozoïque. Palaeovertebrata 24: 177–283.
118. Mazin J-M (1984) Paleobiogeography of the Lower Triassic marine reptiles. In: Reif WE, Westphal F, editors. Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers. Tübingen: Attempto Verlag. pp. 135–140.
119. Maisch MW, Matzke AT (2000) The Ichthyosauria. Stutt Beitr Naturkd Ser B (Geol Pal) 298: 1–159.
120. McGowan C, Motani R (2003) Ichthyopterygia. Handbuch der Paläoherpetologie [Handbook of Paleoherpetology] Part 8: 1–173.
121. Rieppel O (2000) Sauropterygia I - Placodontia, Pachypleurosauria, Nothosauroidea, Pistosauroidea. Handbuch der Paläoherpetologie [Handbook of Paleoherpetology] Part 12A: 1–134.
122. Schoch RR, Milner AR (2000) Vol 3B: Stereospondyli. Handbuch der Paläoherpetologie [Handbook of Paleoherpetology]. München, Germany: F. Pfeil. pp. 1–220.
123. Walker SE, Brett CE (2002) Post-Paleozoic patterns in marine predation: was there a Mesozoic and Cenozoic marine predatory revolution? In: Kowalewski M, Kelley PH, editors. The Fossil Record of Predation. The Paleontological Society Papers 8: 119–193.
124. Kelley NP, Motani R, Jiang D-Y, Rieppel O, Schmitz A (2012) Selective extinction of Triassic marine reptiles during long-term sea-level changes illuminated by seawater strontium isotopes. Palaeogeogr Palaeoclimatol Palaeoecol [doi: 10.1016/j.palaeo.2012.1007.1026].
125. Embry AF (1997) Global sequence boundaries of the Triassic and their identification in the Western Canada Sedimentary Basin. Bull Can Pet Geol 45: 415–433.
126. Rieppel O, Jiang D-Y, Fraser NC, Hao W-C, Motani R, et al. (2010) *Tanystropheus* cf. *T. longobardicus* from the early Late Triassic of Guizhou Province, southwestern China. J Vertebr Paleontol 30: 1082–1089 [doi: 10.1080/02724634.02722010.02483548].

127. Wild R (1974) E. Kuhn-Schnyder und B. Peyer: Die Triasfauna der Tessiner Kalkalpen. XXIII. *Tanystropheus longobardicus* (Bassani) (Neue Ergebnisse). Schweiz Palaeontol Abh 95: 1–162.
128. Wild R (1980) Kuhn-Schnyder, E. & Peyer, B. (eds.) Die Triasfauna der Tessiner Kalkalpen. XXIV. Neue Funde von *Tanystropheus* (Reptilia, Squamata). Schweiz Palaeontol Abh 102: 1–43.
129. Sennikov AG (2011) New tanystropheids (Reptilia: Archosauromorpha) from the Triassic of Europe. Paleontological Journal 45: 90–104 [Original Russian Text © A.G. Sennikov, 2011, published in Paleontologicheskii Zhurnal, 2011, No. 2011, pp. 2082–2096].
130. Motani R (1999) Phylogeny of Ichthyopterygia. J Vertebr Paleontol 19: 473–496.
131. Maisch MW, Matzke AT (2003) Observations on Triassic ichthyosaurs. Part XII. A new Early Triassic ichthyosaur genus from Spitzbergen. N Jb Geol Palaont Abh 229: 317–338.
132. Wiman C (1910) Ein paar Labyrinthodontenreste aus der Trias Spitzbergens. Bull Geol Inst Univ Upsala 9 (1908–1909): 34–40.
133. Wiman C (1914) Über die Stegocephalen aus der Trias Spitzbergens. Bull Geol Inst Univ Upsala 13 (1915–1916): 1–34.
134. Lindemann F-J (1991) Temnospondyls and the Lower Triassic paleogeography of Spitzbergen. In: Kielan-Jaworowska Z, Heintz N, Naktrem HA, editors. Fifth Symposium on Mesozoic Terrestrial Ecosystems and Biota Contributions from the Paleontological Museum, University of Oslo, 364: 39–40.
135. Lindemann F-J (2006) The Early Triassic “Fish Niveau” on Spitzbergen and the habitat of the contained temnospondyls (Amphibia). In: Nakrem HA, Mørk A, editors. Boreal Triassic 2006 (Longyearbyen, Svalbard, 16–19 August 2006) Norsk Geologisk Forening, Abstracts and Proceedings of the Geological Society of Norway. pp. 94–96.
136. Säve-Söderbergh G (1937) On the dermal skulls of *Lyrocephalus*, *Aphaneramma*, and *Benthosaurus*, labyrinthodonts from the Triassic of Spitzbergen and N. Russia. Bull Geol Inst Univ Upsala 27: 189–208.
137. Steyer JS (2002) The first articulated trematosaur ‘amphibian’ from the Lower Triassic of Madagascar: implications for the phylogeny of the group. Palaeontology 45: 771–793 [doi: 10.1111/1475–4983.00260].
138. Welles SP (1993) A review of the lonchorhynchine trematosauroids (Labyrinthodontia), and a description of a new genus and species from the lower Moenkopi Formation of Arizona. PaleoBios 14: 1–24.
139. Noetling F (1901) Beiträge zur Geologie der Salt Range, insbesondere der permischen und triassischen Ablagerungen. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie XIV. Beilageband. 1. Heft: 369–471.
140. Huene Fv (1920) *Gonioglyptus*, ein altriassischer Stegocephale aus Indien. Acta Zool (Stockh) 1: 433–464.
141. Schoch RR, Milner AR, Hellrung H (2002) The last trematosaurid amphibian *Hyperokynodon keuperinus* revisited. Stutt Beitr Naturkd Ser B (Geol Pal) No. 321: 1–9.
142. Säve-Söderbergh G (1935) On the dermal bones of the head in labyrinthodont stegocephalians and primitive Reptilia. Medd Gronl 98: 1–211.
143. Nielsen E (1935) The Permian and Eotriassic vertebrate-bearing beds at Godthaab Gulf (East Greenland). Medd Gronl 98: 1–111.
144. Bjerring HC (1999) A new amphibious tetrapod from the Greenlandic Eotriassic. Copenhagen: Commission for Scientific Research in Greenland. 42 p.
145. Bjerager M, Scidler L, Stemmerik L, Surlyk F (2006) Ammonoid stratigraphy and sedimentary evolution across the Permian–Triassic boundary in East Greenland. Geol Mag 143: 635–656 [doi: 10.1017/S0016756806002020].
146. Perch-Nielsen K, Bromley RG, Birkenmajer K, Aellen M (1972) Field observations in Palaeozoic and Mesozoic sediments of Scoresby Land and Northern Jameson Land. Gronl Geol Unders Rap 48: 39–59.
147. Hewison RH (2007) Journal of Temnospondyl Palaeontology: Skull and Mandible of the Stereospondyl *Lydekkerina* Huxleyi, (Tetrapoda: Temnospondyli) from the Lower Triassic of South Africa, and a Reappraisal of the Family Lydekkerinidae, Its Origin, Taxonomic Relationships and Phylogenetic Importance v.1, No. 1 Minehead: R. H. Hewison. 80 p.
148. Wiman C (1913) Über das Hinterhaupt der Labyrinthodonten. Bull Geol Inst Univ Upsala 12 (1913–1914): 1–8.
149. Wiman C (1916) Neue Stegocephalenfunde aus dem Posidonomyaschiefer Spitzbergens. Bull Geol Inst Univ Upsala 13: 209–222.
150. Weitschat W, Dagens AS (1989) Triassic biostratigraphy of Svalbard and a comparison with NE-Siberia. Mitt Geol-Pal Inst Univ Hamburg 68: 179–213.
151. Buchan SH, Challinor A, Harland WB, Parker JR (1965) The Triassic stratigraphy of Svalbard. Nor Polarinst Skr No.135: 5–92.
152. Cox CB, Smith DG (1973) A review of the Triassic vertebrate faunas of Svalbard. Geol Mag 110: 405–418.
153. Nield CM, Damiani R, Warren A (2006) A short-shouted trematosauroid (Tetrapoda, Temnospondyli) from the Early Triassic of Australia: the oldest known trematosaurine. Alcheringa 30: 263–271 [doi: 10.1080/03115510608619317].
154. Hammer WR (1987) Palaeoecology and phylogeny of the Trematosauridae. In: McKenzie GD, editor. Gondwana Six: Stratigraphy, Sedimentology, and Paleontology American Geophysical Monograph 41, 250, pp. Washington, DC: American Geophysical Union.
155. Fortuny J, Marcé-Nogué J, Esteban-Trivigno Sd, Gil L, Galobart À (2011) Temnospondyli bite club: ecomorphological patterns of the most diverse group of early tetrapods. J Evol Biol 24: 2040–2054 [doi: 10.1111/j.1420-9101.2011.02338.x].
156. Lucas SG, Heckert AB (2000) Biochronological significance of Triassic nonmarine tetrapod records from marine strata. Albertiana 24: 27–32.
157. Maganuco S, Steyer JS, Pasini G, Boulay M, Lorrain S, et al. (2009) An exquisite specimen of *Edingerella madagascariensis* (Temnospondyli) from the Lower Triassic of NW Madagascar; cranial anatomy, phylogeny, and restorations. Mem Soc Ital Sci Nat Mus Civ Storia Nat Milano 36: 1–72.
158. Steyer JS, Boulay M, Lorrain S (2010) 3D external restorations of stegocephalian skulls using ZBrush: the renaissance of fossil amphibians. CR Palevol 9: 463–470 [doi: 10.1016/j.crpv.2010.1007.1007].
159. Lehman J-P (1961) Les Stégocéphales de Madagascar. Ann Pal 47: 42–46.
160. Witzmann F, Soler-Gijón R (2010) The bone histology of osteoderms in temnospondyl amphibians and in the chroniosuchian *Bystrowiella*. Acta Zool (Stockh) 91: 96–114 [doi: 10.1111/j.1463-6395.2008.00385.x].
161. Rieppel O, Hagdorn H (1997) Chapter 5. Paleobiogeography of Middle Triassic Sauropterygia in central and western Europe. In: Callaway JM, Nicholls EL, editors. Ancient Marine Reptiles. San Diego, California: Academic Press. pp. 121–144.
162. Case EC (1936) A nothosaur from the Triassic of Wyoming. Contrib Mus Paleontol Univ Mich 5: 1–36.
163. Rieppel O (1998) *Corosaurus alcovensis* Case and the phylogenetic interrelationships of Triassic stem-group Sauropterygia. Zool J Linn Soc 124: 1–41.
164. Rieppel O (1999) The sauropterygian genera *Chinchenia*, *Kwangsisaurus*, and *Sanchiaosaurus* from the Lower and Middle Triassic of China. J Vertebr Paleontol 19: 321–337 [doi: 10.1080/02724634.02721999.10011144].
165. Galfetti T, Bucher H, Martini R, Hochuli PA, Weissert H, et al. (2008) Evolution of Early Triassic outer platform paleoenvironments in the Nanpanjiang Basin (South China) and their significance for the biotic recovery. Sediment Geol 204: 36–60 [doi: 10.1016/j.sedgeo.2007.1012.1008].
166. Lehrmann DJ, Pei D, Enos P, Minzoni M, Ellwood BB, et al. (2007) Impact of differential tectonic subsidence on isolated carbonate-platform evolution: Triassic of the Nanpanjiang Basin, south China. AAPG Bulletin 91: 287–320 [doi: 10.1306/10160606065].
167. Neenan JM, Klein N, Scheyer TM (2013) European origin of placodont marine reptiles and the evolution of crushing dentition in Placodontia. Nat Commun 4:1621, [doi: 10.1038/ncomms2633].
168. Li J-L, Liu J, Li C, Huang Z-X (2002) The horizon and age of the marine reptiles from Hubei Province, China [in Chinese with English translation]. Vertebr Palasiat 40: 241–244.
169. Jiang D-Y, Motani R, Tintori A, Rieppel O, Sun Z-Y (2012) Two new Early Triassic marine reptiles from Chaochu, Anhui Province, South China. J Vertebr Paleontol, SVP Program and Abstracts Book, 2012: 117.
170. Jiang D-y, Fu W, Motani R, Hao W, Rieppel O, et al. (2013) Diversified Spathian Chaochu fauna from South China. 125th Anniversary Annual Meeting of the Geological Society of America, 27–30 October, 2013, Denver, Colorado, USA.
171. Storrs GW (1991) Anatomy and relationships of *Corosaurus alcovensis* (Diapsida: Sauropterygia) and the Triassic Alcova Limestone of Wyoming. Peabody Mus Nat Hist Yale Univ Bull 44: 1–151.
172. Peyer B (1939) Die Triasfauna der Tessiner Kalkalpen XIV. *Paranothosaurus amleri* nov. gen. nov. spec. Abh Schweiz Palaeontol Ges 62: 1–87.
173. Rieppel O (2002) The dermal armor of the cyamodontoid placodonts (Reptilia, Sauropterygia): morphology and systematic value. Fieldiana Geol NS 46: 1–41.
174. Scheyer TM (2010) New interpretation of the postcranial skeleton and overall body shape of the placodont *Cyamodus hildegardi* Peyer, 1931 (Reptilia, Sauropterygia). Palaeontologia Electronica Vol. 13, Issue 2; 15A:15p. Available: http://palaeo-electronica.org/2010_2/232/index.html.
175. Neenan JM, Scheyer TM (2012) The braincase and inner ear of *Placodus gigas* (Sauropterygia, Placodontia)—a new reconstruction based on micro-computed tomographic data. J Vertebr Paleontol 32: 1350–1357 [doi: 10.1080/02724634.02722012.02695241].
176. Klein N, Scheyer TM (2013) A new placodont sauropterygian from the Middle Triassic of the Netherlands. Acta Palaeontol Polon [doi: 10.4202/app.2012.0147].
177. Mazin J-M (1989) La denture et la région palatine des Placodontia (Reptilia, Trias). Implications phylogénétiques. Geobios 22: 725–734 [doi:10.1016/S0016-6995(1089)80069-80065].
178. Rieppel O (2001) The cranial anatomy of *Placochelys placodonta* Jaekel, 1902, and a review of the Cyamodontioidea (Reptilia, Placodontia). Fieldiana Geol NS 45: 1–104.
179. Rieppel O (2001) Tooth implantation and replacement in Sauropterygia. Palaeontol Z 75: 207–217 [doi:10.1007/BF02988014].
180. Scheyer TM, Neenan JM, Renesto S, Saller F, Hagdorn H, et al. (2012) Revised paleoecology of placodonts – with a comment on ‘The shallow marine placodont *Cyamodus* of the central European Germanic Basin: its evolution, paleobiogeography and paleoecology’ by C.G. Diedrich (Historical Biology, iFirst article, 2011, 1–19, doi: 10.1080/08912963.2011.575938). Hist Biol 24: 257–267 [doi: 10.1080/08912963.08912011.08621083].
181. Merriam JC (1904) A new marine reptile from the Triassic of California. Bull Dept Geol Univ Calif 3: 419–421.
182. Nicholls EL (1999) A reexamination of *Thalattosaurus* and *Nectosaurus* and the relationships of the Thalattosauria (Reptilia: Diapsida). PaleoBios 19: 1–29.
183. Nicholls EL, Brinkman DB (1993) New thalattosaurs (Reptilia: Diapsida) from the Triassic Sulphur Mountain Formation of Wapiti Lake, British Columbia. J Paleontol 67: 263–278.

184. Rieppel O, Müller J, Liu J (2005) Rostral structure in Thalattosauria (Reptilia, Diapsida). *Can J Earth Sci* 42: 2081–2086 [doi: 10.1139/E05-076].
185. Müller J (2005) The anatomy of *Askeptosaurus italicus* from the Middle Triassic of Monte San Giorgio and the interrelationships of thalattosaurs (Reptilia, Diapsida). *Can J Earth Sci* 42: 1347–1367 [doi:10.1139/e1305-1030].
186. Müller J (2007) First record of a thalattosaur from the Upper Triassic of Austria. *J Vertebr Paleontol* 27: 236–240 [doi: 210.1671/0272-4634(2007)1627[1236:FROATF]1672.1670.CO;1672].
187. Callaway JM, Massare JA (1989) Geographic and stratigraphic distribution of the Triassic Ichthyosauria (Reptilia; Diapsida). *N Jb Geol Paläont Abh* 178: 37–58.
188. Maisch MW (2010) Phylogeny, systematics, and origin of the Ichthyosauria – the state of the art. *Palaeodiversity* 3: 151–214.
189. Lucas SG (1997) Marine reptiles and Mesozoic biochronology. In: Callaway JM, Nicholls EL, editors. *Ancient Marine Reptiles*. San Diego, California: Academic Press. pp. 423–434.
190. Mazin J-M, Bucher H (1987) *Omphalosaurus neltarhynchus*, une nouvelle espèce d'Omphalosauridé (Reptilia, Ichthyopterygia) du Spathien de la Humboldt Range (Nevada, U.S.A.). *CR Acad Sci Paris Ser II* 305: 823–828.
191. Mazin JM, Sander PM (1993) Palaeobiogeography of the Early and Late Triassic Ichthyopterygia. *Palaeontologia Lombarda N S* 2: 93–107.
192. Sander PM (2000) Ichthyosauria: their diversity, distribution, and phylogeny. *Palaeontol Z* 74: 1–35 [doi: 10.1007/BF02987949].
193. Thorne PM, Ruta M, Benton MJ (2011) Resetting the evolution of marine reptiles at the Triassic-Jurassic boundary. *Proc Natl Acad Sci USA* 108: 8339–8344 [doi: 8310.1073/pnas.10859108].
194. Mazin J-M, Suteethorn V, Buffetaut E, Jaeger J-J, Helmcke-Ingavat R (1991) Preliminary description of *Thaisaurus chonglakmanii* n. g., n. sp., a new ichthyopterygian (Reptilia) from the Early Triassic of Thailand. *CR Acad Sci Paris Ser II* 313: 1207–1212.
195. Nicholls EL, Brinkman DB (1995) A new ichthyosaur from the Triassic Sulphur Mountain Formation of British Columbia. In: Sarjeant WAS, editor. *Vertebrate Fossils and the Evolution of Scientific Concepts*. Amsterdam: Gordon and Breach Publishers. pp. 521–535.
196. Shikama T, Kamei T, Murata M (1978) Early Triassic ichthyosaurs, *Utatusaurus hataii* gen. et sp. nov., from the Kitakami Massif, Northeast Japan. *Tohoku University, Science Report, 2nd Series (Geology)* 48: 77–97.
197. Wiman C (1929) Eine neue Reptilien-Ordnung aus der Trias Spitzbergens. *Bulletin of the Geological Institutions of the University of Upsala* 22: 183–196.
198. Young CC, Dong ZM (1972) On the Triassic aquatic reptiles of China. *IVPP, Chinese Acad Sci, Memoir* 9: 1–34.
199. Cuthbertson RS, Russell AP, Anderson JS (2013) Cranial morphology and relationships of a new grippidian (Ichthyopterygia) from the Vega-Phroso Siltstone Member (Lower Triassic) of British Columbia, Canada. *J Vertebr Paleontol* 33: 831–847 [doi: 810.1080/02724634.02722013.02755989].
200. Brinkman DB, Zhao X, Nicholls EL (1992) A primitive ichthyosaur from the Lower Triassic of British Columbia, Canada. *Palaeontology* 35: 465–474.
201. Motani R (1997) Phylogeny of the Ichthyosauria (Amniota: Reptilia) with special reference to Triassic forms. *PhD thesis*. Toronto: University of Toronto. 384 p.
202. Sander PM, Faber C (2003) The Triassic marine reptile *Omphalosaurus*: osteology, jaw anatomy, and evidence for ichthyosaurian affinities. *J Vertebr Paleontol* 23: 799–816 [doi: 710.1671/1676].
203. Motani R (2000) Skull of *Grippia longirostris*: no contradiction with a diapsid affinity for the Ichthyopterygia. *Palaeontology* 43: 1–14.
204. Harland WB (1997) The Geology of Svalbard. *Geological Society Memoir No. 17*. London: The Geological Society. 521 p.
205. Mork A, Elvebakk G, Forsberg AW, Hounslow MW, Nakrem HA, et al. (1999) The type section of the Vikinghogda Formation: a new Lower Triassic unit in central and eastern Svalbard. *Polar Research* 18: 51–82.
206. Massare JA (1987) Tooth morphology and prey preference of Mesozoic marine reptiles. *J Vertebr Paleontol* 7: 121–137.
207. Motani R (1996) Redescription of the dental features of an Early Triassic ichthyosaur, *Utatusaurus hataii*. *J Vertebr Paleontol* 16: 396–402.
208. Motani R (1997) Redescription of the dentition of *Grippia longirostris* (Ichthyosauria) with a comparison with *Utatusaurus hataii*. *J Vertebr Paleontol* 17: 39–44 [doi: 10.1080/02724634.02721997.10010951].
209. Maxwell EE, Kear BP (2013) Triassic ichthyopterygian assemblages of the Svalbard Archipelago: a reassessment of taxonomy and distribution. *GFF* 135: 85–94 [doi: 10.1080/11035897.11032012.11759145].
210. Motani R, Minoura N, Ando T (1998) Ichthyosaurian relationships illuminated by new primitive skeletons from Japan. *Nature* 393: 255–257.
211. Nicholls EL, Brinkman D (1993) A new specimen of *Utatusaurus* (Reptilia: Ichthyosauria) from the Lower Triassic Sulphur Mountain Formation of British Columbia. *Can J Earth Sci* 30: 486–490.
212. Balini M, Lucas SG, Jenks JF, Spielmann JA (2010) Triassic ammonoid biostratigraphy: an overview. *Geol Soc London Spec Publ* 334: 221–262 [doi: 210.1144/SP1334.1110].
213. Motani R, You H (1998) Taxonomy and limb ontogeny of *Chaohosaurus geishanensis* (Ichthyosauria), with a note on the allometric equation. *J Vertebr Paleontol* 18: 533–540.
214. Motani R, You H, McGowan C (1996) Eel-like swimming in the earliest ichthyosaurs. *Nature* 382: 347–348 [doi:10.1038/382347a382340].
215. Chen X, Sander PM, Cheng L, Wang X (2013) A new Triassic primitive ichthyosaur from Yuanan, South China. *Acta Geologica Sinica (English Edition)* 87: 672–677 [doi: 10.1111/1755-6724.12078].
216. Merriam JC (1906) Preliminary note on a new marine reptile from the Middle Triassic of Nevada. *Bull Dept Geol Univ Calif* 5: 75–79.
217. Motani R (2000) Is *Omphalosaurus* ichthyopterygian?—A phylogenetic perspective. *J Vertebr Paleontol* 20: 295–301 [doi: 210.1671/0272-4634(2000)1020 [0295:IOIAPP]1672.1670.CO;1672].
218. Bucher H (1989) Lower Anisian ammonoids from the northern Humboldt Range (northwestern Nevada, USA) and their bearing upon the Lower-Middle Triassic boundary. *Eclogae Geol Helv* 82: 943–1002.
219. Tichy G (1995) Ein früher, durophager Ichthyosaurier (Omphalosauridae) aus der Mitteltrias der Alpen. *Geologisch-Paläontologische Mitteilungen, Innsbruck* 20: 349–369.
220. Sander PM, Faber C (1998) New finds of *Omphalosaurus* and a review of Triassic ichthyosaur paleobiogeography. *Palaeontol Z* 72: 149–162 [doi: 110.1007/BF02987823].
221. Maisch MW, Matzke AT (2002) The skull of a large Lower Triassic ichthyosaur from Spitzbergen and its implications for the origin of the Ichthyosauria. *Lethaia* 35: 250–256 [doi: 10.1111/j.1502-3931.2002.tb00082.x].
222. Motani R (2005) Evolution of fish-shaped reptiles (Reptilia: Ichthyopterygia) in their physical environments and constraints. *Annu Rev Earth Planet Sci* 33: 395–420 [doi: 310.1146/annurev.earth.1133.092203.122707].
223. Brinkmann W (2004) Mixosaurier (Reptilia, Ichthyosauria) mit Quetschzähnen aus der Grenzbitumenzone (Mitteltrias) des Monte San Giorgio (Schweiz, Kanton Tessin). *Schweiz Palaeontol Abh* 124: 1–84.
224. Massare JA, Callaway JM (1990) The affinities and ecology of Triassic ichthyosaurs. *Geol Soc Am Bull* 102: 409–416 [doi: 410.1130/0016-7606(1990)1102<0409:TAAEOT>1132.1133.CO;1132].
225. Jiang D, Motani R, Hao W, Schmitz L, Rieppel O, et al. (2008) New primitive ichthyosaurian (Reptilia, Diapsida) from the Middle Triassic of Panxian, Guizhou, southwestern China and its position in the Triassic biotic recovery. *Progress in Natural Science* 18: 1315–1319 [doi:1310.1016/j.pnsc.2008.1301.1039].
226. Wiman C (1910) Ichthyosaurier aus der Trias Spitzbergens. *Bull Geol Inst Univ Upsala* 10 (1910–1911): 124–148.
227. Maisch MW, Matzke AT (2002) Observations on Triassic ichthyosaurs. Part IX. The first associated skeletal remains of *Merriamosaurus* n. g. (Ichthyosauria, Lower Triassic) and their bearing on the systematic position of the Omphalosauria. *N Jb Geol Paläont Abh* 226: 59–94.
228. Maisch MW, Matzke AT (2003) Observations on Triassic ichthyosaurs, Part X: The Lower Triassic *Merriamosaurus* from Spitzbergen - additional data on its anatomy and phylogenetic position. *N Jb Geol Paläont Abh* 227: 93–137.
229. Mazin JM (1981) *Svalbardosaurus crassidens* n.g., n.sp., un Ichthyopterygien nouveau du Spathien (Trias inférieur) du Spitzberg. *CR Acad Sci, Paris* 293: 203–205.
230. Mazin J-M, Martin M (1984) Marine reptiles and fishes as a test for the paleobiogeography of the Lower and Middle Triassic. In: Reif WE, Westphal F, editors. *Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*. Tübingen: Attempto Verlag. pp. 141–144.
231. Kelley NP, Motani R, Embree PG (2012) A new Lower Triassic ichthyopterygian fauna from Fossil Hill, Nevada. *J Vertebr Paleontol*, SVP Program and Abstracts Book, 2012: 120.
232. Massare JA, Callaway JM (1994) *Cymbospondylus* (Ichthyosauria: Shastasauridae) from the Lower Triassic Thaynes Formation of Southeastern Idaho. *J Vertebr Paleontol* 14: 139–141.
233. Balini M, Renesto SC (2012) *Cymbospondylus* vertebrae (Ichthyosauria, Shastasauridae) from the Upper Anisian Prezzo Limestone (Middle Triassic, southern Alps) with an overview of the chronostratigraphic distribution of the group. *Rivista Italiana di Paleontologia e Stratigrafia* 118: 155–172.
234. Nicholls EL, Manabe M (2004) Giant ichthyosaurs of the Triassic—A new species of *Shonisaurus* from the Pardonet Formation (Norian: Late Triassic) of British Columbia. *J Vertebr Paleontol* 24: 838–849 [doi: 810.1671/0272-4634(2004)1024[0838:GIOTTN]1672.1670.CO;1672].
235. Sander PM, Chen X, Long C, Wang X (2011) Short-snouted toothless ichthyosaur from China suggests Late Triassic diversification of suction feeding ichthyosaurs. *PLoS ONE* 6(5): e19480 [doi:10.1371/journal.pone.0019480].
236. Fröbisch NB, Fröbisch J, Sander PM, Schmitz L, Rieppel O (2013) A macropredatory ichthyosaur from the Middle Triassic and the origin of modern trophic networks. *Proc Natl Acad Sci USA* 110: 1393–1397 [doi: 1310.1073/pnas.1216750110].
237. Motani R (1999) On the evolution and homologies of ichthyopterygian forefins. *J Vertebr Paleontol* 19: 28–41.
238. Nicholls EL, Manabe M (2001) A new genus of ichthyosaur from the Late Triassic Pardonet Formation of British Columbia: bridging the Triassic-Jurassic gap. *Can J Earth Sci* 38: 983–1002 [doi: 10.1139/c00-115].
239. Callaway JM, Massare JA (1989) *Shastasaurus altispinus* (Ichthyosauria, Shastasauridae) from the Upper Triassic of the El Antimonio District, Northwestern Sonora, Mexico. *J Paleontol* 63: 930–939.
240. Cuthbertson RS, Russell AP, Anderson JS (2013) Reinterpretation of the cranial morphology of *Utatusaurus hataii* (Ichthyopterygia) (Osawa Formation, Lower Triassic, Miyagi, Japan) and its systematic implications. *J Vertebr Paleontol* 33: 817–830 [doi: 810.1080/02724634.02722013.02756495].

241. Nicholls EL, Brinkman DB, Callaway JM (1999) New material of *Phalarodon* (Reptilia: Ichthyosauria) from the Triassic of British Columbia and its bearings on the interrelationships of mixosaurs. *Palaentogr Abt A* 252: 1–22.
242. Sander PM (1989) The large ichthyosaur *Cymbospondylus buchseri*, sp. nov., from the Middle Triassic of Monte San Giorgio (Switzerland), with a survey of the genus in Europe. *J Vertebr Paleontol* 9: 163–173.
243. Merriam JC (1908) Triassic Ichthyosauria, with special reference to the American forms. *Memoirs of the University of California* 1: 1–155.
244. Leidy J (1868) Notice of some reptilian remains from Nevada. *Proc Acad Nat Sci Philad* 20: 177–178.
245. Hogler JA (1992) Taphonomy and paleoecology of *Shonisaurus popularis* (Reptilia: Ichthyosauria). *Palaos* 7: 108–117.
246. Kosch BF (1990) A revision of the skeletal reconstruction of *Shonisaurus popularis* (Reptilia: Ichthyosauria). *J Vertebr Paleontol* 10: 512–514.
247. Yin G, Zhou X, Cao Z, Yu Y, Luo Y (2000) A preliminary study on the early Late Triassic marine reptiles from Guanling, Guizhou, China [in Chinese with English summary]. *Geology-Geochemistry* 28: 1–23.
248. Cheng L, Wings O, Chen X, Sander PM (2006) Gastroliths in the Triassic ichthyosaur *Panjiangsaurus* from China. *J Paleontol* 80: 583–588 [doi: 10.1666/0022-3360(2006)1680[1583:GITTIP]1662.1660.CO;1662].
249. Shang Q-H, Li C (2009) On the occurrence of the ichthyosaur *Shastasaurus* in the Guanling Biota (Late Triassic), Guizhou, China. *Vertebr Palasiat* 47: 178–193.
250. Motani R, Manabe M, Dong Z-M (1999) The status of *Himalayasaurus tibetensis* (Ichthyopterygia). *Paludicola* 2: 174–181.
251. Dong Z-M (1972) An ichthyosaur fossil from the Qomolangma Feng region. In: Young CC, Dong ZM, editors. *Aquatic reptiles from the Triassic of China* Academia Sinica. IVPP Memoir 9, Peking [in Chinese]. pp. 7–10.
252. McGowan C (1996) Giant ichthyosaurs of the Early Jurassic. *Can J Earth Sci* 33: 1011–1021 [doi: 10.1139/e1096-1077].
253. Theodori C (1854) Beschreibung des kolossalen *Ichthyosaurus trigonodon* in der Lokal-Petrefakten-Sammlung zu Banz, nebst synoptischer Darstellung der übrigen *Ichthyosaurus*-Arten in derselben. München: Georg Franz. XVII + 81 p.
254. Motani R, Ji C, Tomita T, Kelley N, Maxwell E, et al. (2013) Absence of suction feeding ichthyosaurs and its implications for Triassic mesopelagic paleoecology. *PLoS ONE* 8(12): e66075 [doi:10.1371/journal.pone.0066075].
255. Bernard A, Lécuyer C, Vincent P, Amiot R, Bardet N, et al. (2010) Regulation of body temperature by some Mesozoic marine reptiles. *Science* 328: 1379–1382 [doi: 1310.1126/science.1187443].
256. Motani R (2010) Warm-blooded “sea dragons”? *Science* 328: 1361–1362 [doi: 1310.1126/science.1191409].
257. Carroll RL, Dong Z-M (1991) *Hupehsuchus*, an enigmatic aquatic reptile from the Triassic of China, and the problem of establishing relationships. *Phil Trans R Soc Lond B* 331: 131–153.
258. Wang K (1959) Ueber eine neue fossile Reptilform von Provinz Hupeh, China. *Acta Palaentol Sin* 7: 373–378.
259. Motani R (2009) The evolution of marine reptiles. *Evolution: Education and Outreach* 2: 224–235 [doi: 210.1007/s12052-12009-10139-y].
260. Wu X-C, Li Z, Zhou B-C, Dong Z-M (2003) A polydactylous amniote from the Triassic period. *Nature* 426: 516 [doi: 10.1038/426516a].
261. Kauffman EG, Harries PJ (1996) The importance of crisis progenitors in recovery from mass extinction. In: Hart MB, editor. *Biotic Recovery from Mass Extinction Events*. *Geol Soc Spec Publ* No 102. pp. 15–39.
262. Gheerbrant E, Domning DP, Tassy P (2005) Paenungulata (Sirenia, Proboscidea, Hyracoidea, and relatives). In: Rose KD, Archibald JD, editors. *The Rise Of Placental Mammals: Origins And Relationships Of The Major Extant Clades*. Baltimore: Johns Hopkins University Press. pp. 84–105.
263. Gingerich PD (2005) Cetacea. In: Rose KD, Archibald JD, editors. *The Rise of Placental Mammals*. Baltimore: Johns Hopkins University Press. pp. 234–252.
264. Gingerich PD, Raza SM, Arif M, Anwar M, Zhou X (1994) New whale from the Eocene of Pakistan and the origin of cetacean swimming. *Nature* 368: 844–847.
265. Gingerich PD, Russell DE (1981) *Pakicetus inachus*, A new archaeocete (Mammalia, Cetacea) from the Early-Middle Eocene Kuldana Formation of Kohat (Pakistan). *Contrib Mus Paleontol Univ Mich* 25: 235–246.
266. Hulbert RC Jr, Petkewich RM, Bishop GA, Bukry D, Aleshire DP (1998) A new Middle Eocene protocetid whale (Mammalia: Cetacea: Archaeoceti) and associated biota from Georgia. *J Paleontol* 72: 907–927.
267. Savage RJG, Domning DP, Thewissen JGM (1994) Fossil Sirenia of the West Atlantic and Caribbean Region. V. the most primitive known sirenian, *Proastomus sirenioides* Owen, 1855. *J Vertebr Paleontol* 14: 427–449.
268. Domning DP (2001) The earliest known fully quadrupedal sirenian. *Nature* 413: 625–627 [doi: 10.1038/35098072].
269. Ovtcharova M, Goudemand N, Galfetti T, Brayard A, Kuang G, et al. (2013) Improved radio-isotopic and biochronological approaches: application to the Early-Middle Triassic boundary. 125th Anniversary Annual Meeting of the Geological Society of America, 27–30 October, 2013, Denver, Colorado, USA.
270. Organ CL, James DE, Meade A, Pagel M (2009) Genotypic sex determination enabled adaptive radiations of extinct marine reptiles. *Nature* 461: 389–392 [doi: 310.1038/nature08350].
271. Chin K (2002) Analyses of coprolites produced by carnivorous vertebrates. In: Kowalewski M, Kelley PH, editors. *The Fossil Record of Predation*. The Paleontological Society Papers 8: 43–49.
272. McAllister J (2003) Predation of fishes in the fossil record. In: Kelley PH, Kowalewski M, Hansen T, editors. *Predator-Prey Interactions in the Fossil Record [Topics in Geobiology, Volume 20]*. New York: Kluwer Academic/Plenum Publishers. pp. 303–324.
273. Benson RBJ, Butler RJ (2011) Uncovering the diversification history of marine tetrapods: ecology influences the effect of geological sampling biases. In: McGowan AJ, Smith AB, editors. *Comparing the Geological and Fossil Records: Implications for Biodiversity Studies*. *Geol Soc London Spec Publ* 358: 191–208 [doi: 10.1144/SP35813].
274. Rothschild BM, Xiaoting Z, Martin LD (2012) Adaptations for marine habitat and the effect of Triassic and Jurassic predator pressure on development of decompression syndrome in ichthyosaurs. *Naturwissenschaften* 99: 443–448 [doi: 410.1007/s00114-00012-00918-00110].
275. Young C-C (1958) On the new *Pachypleurosauroidea* from Keichow, South-West China. *Vertebr Palasiat* 2: 69–81.
276. Li C (2010) Amazing reptile fossils from the marine Triassic of China. *Bull Chinese Acad Sci* 24: 80–82.
277. Liu H-T (1964) A new coelacanth from the marine Lower Triassic of N.W. Kwangsi, China. *Vertebr Palasiat* 8: 213–215.
278. Su T-T (1959) Triassic fishes from Kueichow, south-west China. *Vertebr Palasiat* 3: 205–212.
279. Su D (1981) A new species of *Perleidus* from Anhui. *Vertebr Palasiat* 19: 107–112. [in Chinese with English summary].
280. Sun Z-Y, Tintori A, Lombardo C, Jiang D-Y, Hao W-C, et al. (2008) A new species of the genus *Colobodus* Agassiz, 1844 (Osteichthyes, Actinopterygii) from the Pelsonian (Anisian, Middle Triassic) of Guizhou, South China. *Rivista Italiana di Paleontologia e Stratigrafia* 114: 363–376.
281. Sun Z-Y, Tintori A, Jiang D-Y, Lombardo C, Rusconi M, et al. (2009) A new perleidiform (Actinopterygii, Osteichthyes) from the middle Anisian (Middle Triassic) of Yunnan, South China. *Acta Geologica Sinica* 83: 460–470 [doi: 10.1111/j.1755-6724.2009.00067.x].
282. Tintori A, Sun Z-Y, Lombardo C, Jiang D-Y, Sun Y-L, et al. (2010) A new basal neopterygian from the Middle Triassic of Luoping County (South China). *Rivista Italiana di Paleontologia e Stratigrafia* 116: 161–172.
283. Carroll RL (1981) Plesiosaur ancestors from the Upper Permian of Madagascar. *Phil Trans R Soc Lond B* 293: 315–383.
284. Currie PJ (1981) *Hovasauros boulei*, an aquatic cosuchian from the Upper Permian of Madagascar. *Paleontologia africana* 24: 99–168.
285. Piveteau J (1926) *Paleontologie de Madagascar, XIII. Amphibiens et reptiles permien*. *Ann Pal* 15: 53–180.
286. Ketchum HF, Barrett PM (2004) New reptile material from the Lower Triassic of Madagascar: implications for the Permian–Triassic extinction event. *Can J Earth Sci* 41: 1–8 [doi: 10.1139/e03-084].
287. Spath LF (1934) Catalogue of the fossil Cephalopoda in the British Museum (Natural History). Part IV The Ammonoidea of the Trias. London: The Trustees of the British Museum. 521 pp.
288. Warren AA (2000) Secondly aquatic temnospondyls of the Upper Permian and Mesozoic. In: Heatwole H, Carroll RL, editors. *Amphibian Biology*, Vol 4, *Palaentology: The Evolutionary History of Amphibians*. Chipping Norton: Surrey Beatty & Sons. pp. 1121–1149.
289. Schuch RR (2011) A trematosauroid temnospondyl from the Middle Triassic of Jordan. *Fossil Record* 14: 119–127 [doi: 110.1002/mnng.201100002].
290. Galfetti T, Bucher H, Brayard A, Hochuli PA, Weissert H, et al. (2007) Late Early Triassic climate change: Insights from carbonate carbon isotopes, sedimentary evolution and ammonoid paleobiogeography. *Palaogeogr Palaoclimatol Palaecoecol* 243: 394–411 [doi: 310.1016/j.palaeo.2006.1008.1014].
291. Bucher H, Hochuli PA, Goudemand N, Schneebeil-Hermann E, Romano C, et al. (2013) Some like it hot: the Smithian diversification-extinction model. 125th Anniversary Annual Meeting of the Geological Society of America, 27–30 October, 2013, Denver, Colorado, USA.
292. Galfetti T, Hochuli PA, Brayard A, Bucher H, Weissert H, et al. (2007) Smithian-Spathian boundary event: Evidence for global climatic change in the wake of the end-Permian biotic crisis. *Geology* 35: 291–294 [doi: 210.1130/G23117A.23111].

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	AA	AB	AC	AD	AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	AR	AS	AT	AU	AV	AW	AX	AY	AZ	BA	BB	BC	BD	BE	BF	BG	BH	BI	BJ	BK	BL	BM	BN	BO	BP	BQ	BR	BS	BT	BU	BV	BW	BX	BY	BZ	CA	CB	CC	CD	CE	CF	CG	CH	CI	CJ	CK	CL	CM	CN	CO	CP	CQ	CR	CS	CT	CU	CV	CW	CX	CY	CZ	DA	DB	DC	DD	DE	DF	DG	DH	DI	DJ	DK	DL	DM	DN	DO	DP	DQ	DR	DS	DT	DU	DV	DW	DX	DY	DZ	EA	EB	EC	ED	EE	EF	EG	EH	EI	EJ	EK	EL	EM	EN	EO	EP	EQ	ER	ES	ET	EU	EV	EW	EX	EY	EZ	FA	FB	FC	FD	FE	FF	FG	FH	FI	FJ	FK	FL	FM	FN	FO	FP	FQ	FR	FS	FT	FU	FV	FW	FX	FY	FZ	GA	GB	GC	GD	GE	GF	GG	GH	GI	GJ	GK	GL	GM	GN	GO	GP	GQ	GR	GS	GT	GU	GV	GW	GX	GY	GZ	HA	HB	HC	HD	HE	HF	HG	HH	HI	HJ	HK	HL	HM	HN	HO	HP	HQ	HR	HS	HT	HU	HV	HW	HX	HY	HZ	IA	IB	IC	ID	IE	IF	IG	IH	II	IJ	IK	IL	IM	IN	IO	IP	IQ	IR	IS	IT	IU	IV	IW	IX	IY	IZ	JA	JB	JC	JD	JE	JF	JG	JH	JI	JJ	JK	JL	JM	JN	JO	JP	JQ	JR	JS	JT	JU	JV	JW	JX	JY	JZ	KA	KB	KC	KD	KE	KF	KG	KH	KI	KJ	KL	KM	KN	KO	KP	KQ	KR	KS	KT	KU	KV	KW	KX	KY	KZ	LA	LB	LC	LD	LE	LF	LG	LH	LI	LJ	LK	LM	LN	LO	LP	LQ	LR	LS	LT	LU	LV	LW	LX	LY	LZ	MA	MB	MC	MD	ME	MF	MG	MH	MI	MJ	MK	ML	MM	MN	MO	MP	MQ	MR	MS	MT	MU	MV	MW	MX	MY	MZ	NA	NB	NC	ND	NE	NF	NG	NH	NI	NJ	NK	NL	NM	NN	NO	NP	NQ	NR	NS	NT	NU	NV	NW	NX	NY	NZ	OA	OB	OC	OD	OE	OF	OG	OH	OI	OJ	OK	OL	OM	ON	OO	OP	OQ	OR	OS	OT	OU	OV	OW	OX	OY	OZ	PA	PB	PC	PD	PE	PF	PG	PH	PI	PJ	PK	PL	PM	PN	PO	PP	PQ	PR	PS	PT	PU	PV	PW	PX	PY	PZ	QA	QB	QC	QD	QE	QF	QG	QH	QI	QJ	QK	QL	QM	QN	QO	QP	QQ	QR	QS	QT	QU	QV	QW	QX	QY	QZ	RA	RB	RC	RD	RE	RF	RG	RH	RI	RJ	RK	RL	RM	RN	RO	RP	RQ	RR	RS	RT	RU	RV	RW	RX	RY	RZ	SA	SB	SC	SD	SE	SF	SG	SH	SI	SJ	SK	SL	SM	SN	SO	SP	SQ	SR	SS	ST	SU	SV	SW	SX	SY	SZ	TA	TB	TC	TD	TE	TF	TG	TH	TI	TJ	TK	TL	TM	TN	TO	TP	TQ	TR	TS	TU	TW	TX	TY	TZ	UA	UB	UC	UD	UE	UF	UG	UH	UI	UJ	UK	UL	UM	UN	UO	UP	UQ	UR	US	UT	UU	UV	UW	UX	UY	UZ	VA	VB	VC	VD	VE	VF	VG	VH	VI	VJ	VK	VL	VM	VN	VO	VP	VQ	VR	VS	VT	VU	VV	VW	VX	VY	VZ	WA	WB	WC	WD	WE	WF	WG	WH	WI	WJ	WK	WL	WM	WN	WO	WP	WQ	WR	WS	WT	WU	WV	WW	WX	WY	WZ	XA	XB	XC	XD	XE	XF	YG	YH	YI	YJ	YK	YL	YM	YN	YO	YP	YQ	YR	YS	YT	YU	YV	YW	YX	YY	YZ	ZA	ZB	ZC	ZD	ZE	ZF	ZG	ZH	ZI	ZJ	ZK	ZL	ZM	ZN	ZO	ZP	ZQ	ZR	ZS	ZT	ZU	ZV	ZW	ZX	ZY	ZZ	AA	AB	AC	AD	AE	AF
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rB			
1	<i>Chaohusaurus geishanensis</i> Young & Dong, 1972	Spathian	740
2	<i>Chaohusaurus zhangjiawanensis</i> Chen, Sander, Cheng & Wang, 2013	Spathian/Anisian?	630
3	<i>Corosaurus alcovensis</i> Case, 1936	Spathian	1650
4	<i>Edingerella madagascariensis</i> (Lehman, 1961)	Lowermost Olenekian	600
5	<i>Hupehsuchus nanchangensis</i> Young & Dong, 1972	Spathian/Anisian?	730
6	<i>Ichthyopterygia</i> indet. (new giant humerus)	early Spathian	11000
7	<i>Keichousaurus yunanensis</i> Young, 1965	Spathian/Anisian?	217
8	<i>Nanchangosaurus suni</i> Wang, 1959	Spathian/Anisian?	350
9	<i>Neodiapsida</i> indet. (yet undescribed new material)	Spathian	1400
10	<i>Utatsusaurus hataii</i> Shikama, Kamei & Murata, 1978	Spathian	2600
11	<i>Wantosaurus elongatus</i> Lehman, 1961	Griesbachian	1500

MDDRA RRD			
1	<i>Anshunsaurus wushaensis</i> Rieppel, Liu & Li, 2006	Ladinian (Longobardian)	2600
2	<i>Askeptosaurus italicus</i> Nopsca, 1925	Ladinian (Fassanian)	3000
3	<i>Besanosaurus leptorhynchus</i> Dal Sasso & Pinna, 1996	Anisian (Illyrian)	4330
4	<i>Ceresiosaurus calcagnii</i>	Ladinian (Fassanian)	2470
5	<i>Ceresiosaurus lanzi</i>	Ladinian (Fassanian)	1820
6	<i>Clarazia schinzi</i> Peyer, 1936	Anisian/Ladinian (Illyrian/Fassanian)	1000
7	<i>Cyamodus hildegardis</i>	Ladinian (Fassanian)	1160
8	<i>Cymbospondylus buchseri</i> Sander, 1989	Anisian (Illyrian)	5000
9	<i>Cymbospondylus piscosus</i> Leidy, 1868	Anisian (Illyrian)	9300
10	<i>Dactylosaurus gracilis</i>	Anisian (Aegean)	390
11	<i>Dianlongosaurus acutidentatus</i> Shang, Wu & Li, 2011	Anisian (Pelsonian)	340
12	<i>Dianopachysaurus dingi</i>	Anisian (Pelsonian)	140
13	<i>Dinocephalosaurus orientalis</i> Li, 2003	Anisian (Pelsonian)	2700
14	<i>Glyphoderma kangii</i>	Ladinian (Longobardian)	870
15	<i>Helveticosaurus zollingeri</i> Peyer, 1955	Anisian/Ladinian (Illyrian/Fassanian)	2000
16	<i>Keichousaurus hui</i>	Ladinian (Longobardian)	350
17	<i>Largocephalosaurus qianensis</i> Li, Jiang, Cheng, Wu & Rieppel, 2013	Anisian (Pelsonian)	2320
18	<i>Lariosaurus balsami</i>	Ladinian (Longobardian)	870
19	<i>Lariosaurus buzzii</i> Tschanz, 1989	Ladinian (Fassanian)	1000
20	<i>Lariosaurus hongguoensis</i>	Anisian (Pelsonian)	580
21	<i>Lariosaurus valceresii</i> Tintori & Renesto, 1990	Ladinian (Longobardian)	900
22	<i>Lariosaurus xingyiensis</i>	Ladinian (Longobardian)	1800
23	<i>Mixosaurus cornalianus</i> (Bassani, 1886)	Anisian (Illyrian)	980
24	<i>Mixosaurus panxianensis</i> Jiang, Schmitz, Hao & Sun, 2006	Anisian (Pelsonian)	728
25	<i>Neusticosaurus edwardsii</i>	Ladinian (Fassanian)	1200
26	<i>Neusticosaurus peyeri</i>	Ladinian (Fassanian)	500
27	<i>Neusticosaurus pusillus</i>	Ladinian (Fassanian)	460
28	<i>Neusticosaurus staubi</i>	Ladinian (Longobardian)	500
29	<i>Nothosaurus giganteus</i>	Anisian (Illyrian)	3850
30	<i>Nothosaurus jagisteus</i> Rieppel, 2001	Ladinian (Fassanian)	920
31	<i>Nothosaurus rostellatus</i> Shang, 2006	Anisian (Pelsonian)	1020
32	<i>Nothosaurus youngi</i> Li & Rieppel, 2004	Ladinian (Longobardian)	650
33	<i>Parapilacodus broilii</i> Peyer, 1931	Ladinian	1400
34	<i>Pararcus diepenbroeki</i> Klein & Scheyer, 2013	Anisian (Bithynian/Pelsonian)	1350
35	<i>Phalarodon atavus</i> (Quenstedt, 1852)	Anisian (Pelsonian)	500
36	<i>Phalarodon callawayi</i> Schmitz, Sander, Storrs & Rieppel, 2004	Anisian (Illyrian)	1500
37	<i>Phalarodon fraasi</i> Merriam, 1910	Anisian (Pelsonian)	2800
38	<i>Phantomasaurus neubigi</i> (Sander, 1997)	Anisian (Illyrian)	3000
39	<i>Pistosaurus longaevus</i> Meyer, 1839	Anisian (Illyrian)	2080
40	<i>Placodus gigas</i> Agassiz, 1833	Anisian (Bithynian)	2500
41	<i>Placodus inexpectatus</i> Jiang, Motani, Hao, Rieppel, Sun, Schmitz & Sun, 2008	Anisian (Pelsonian)	2050
42	<i>Qianosuchus mixtus</i> Li, Wu, Cheng, Sato & Wang, 2006	Anisian (Pelsonian)	3000
43	<i>Qianxisaurus chajiangensis</i> Cheng, Wu, Sato & Shan, 2012	Ladinian (Longobardian)	760
44	<i>Sanchiaosaurus dengi</i> Young, 1965	Anisian (Aegean?)	700
45	<i>Serpianosaurus mirigiolensis</i> Rieppel, 1989	Anisian/Ladinian (Illyrian/Fassanian)	750
46	<i>Simosaurus gaillardoti</i> Meyer, 1842	Ladinian (Fassanian)	3500
47	<i>Tanystropheus longobardicus</i> Bassani, 1886	Anisian/Ladinian (Illyrian/Fassanian/Longobardian)	4200
48	<i>Thalattoarchon saurophagus</i> Fröbisch, Fröbisch, Sander, Schmitz & Rieppel, 2013	Anisian (Pelsonian)	8600
49	<i>Wumengosaurus delicatmandibularis</i> Jiang, Rieppel, Motani, Hao, Sun, Schmitz & Sun, 2008	Anisian (Pelsonian)	960
50	<i>Xinminosaurus catactes</i> Jiang, Motani, Hao, Schmitz, Rieppel, Sun & Sun, 2008	Anisian (Pelsonian)	2320
51	<i>Yunguisaurus liae</i> Cheng, Sato, Wu and Li, 2006	Ladinian (Longobardian)	4016

A dReferences accompanying Appendices S1-S2.

R r**A d**

- Abel O (1906) Fossile Flugfische. Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt 56 (1): 1–88.
- Alessandri Gd (1910) Studii sui pesci Triasici della Lombardia. Memorie della Società italiana di Scienza naturale 7(1): 1–147.
- Andersson (= Stensiö) E (1916) Beschreibung einiger Fischreste aus Madagaskar und Siam. Bulletin of the Geological Institution of the University of Upsala 13: 227–232.
- Bashkuev A, Sell J, Aristov D, Ponomarenko A, Sinitshenkova N. Mahler H (2012) Insects from the Buntsandstein of Lower Franconia and Thuringia. Paläontologische Zeitschrift 86(2): 175–185.
- Bassani F (1886) Sui fossili e sull'età degli schisti bituminosi Triasici di Besano in Lombardia. Comunicazione preliminare. Atti della Società Italiana di Scienze Naturale 29: 15–72.
- Bellotti C (1857) Descrizione di alcune nuove specie di pesci fossili di Perledo e di altre località lombarde. In: Stoppani A, editor. Studii Geologici e Paleontologici sulla Lombardia. Milano: Turati. pp. 419–438.
- Bellotti C (1873) Osservazioni alla collezione dei pesci fossili del Museo civico. Dal catalogo manoscritto del 1873: 27–30. [Reprinted in: Pinna, G (1991) I primi studi sui pesci fossili triassici della Lombardia al Museo di Storia Naturale di Milano. Natura: Rivista di Scienze Naturali 82: 1–41.]
- Beltan L (1968) La faune ichthyologique de l'Eotrias du N.W. de Madagascar: le neurocrâne. CNRS, Paris: Cahiers de paléontologie. 135 p.

- Beltan L (1977) La parturition d'un actinoptérygien de l'Eotrias du nord-ouest de Madagascar. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris 284: 2223–2225.
- Beltan L (1980) Eotrias du nord-ouest de Madagascar: Etude de quelques poissons, dont un est en parturition. Annales de la Société Géologique du Nord 99: 453–464.
- Beltan L (1984) A propos d'un poisson Volant biplane de l'Eotrias du NW de Madagascar. Annales de la Société Géologique du Nord 103: 75–82.
- Beltan L, Janvier P (1978) Un nouveau Saurichthyidae (Pisces, Actinopterygii), *Saurichthys nepalensis* n. sp., du Trias inférieur des Annapurnas (Thakkhola, Nepal) et sa signification paléobiogéographique. Cybium 3(4): 17–28.
- Berg LS, Kazantseva AA, Obruchev DV (1967) Superorder Palaeonisci (Archistia). In: Obruchev DV, editor. Fundamentals of Paleontology, 11, Agnatha, Pisces. Jerusalem: Israel Program for Scientific Translation. pp. 528–573. [Translated from Russian, published in Russian 1964: Osnovy paleontologii]
- Brough J (1939) The Triassic fishes of Besano, Lombardy. London: British Museum (Natural History). 117 p.
- Bürgin T (1992) Basal ray-finned fishes (Osteichthyes; Actinopterygii) from the Middle Triassic of Monte San Giorgio (Canton Tessin, Switzerland). Systematic palaeontology with notes on functional morphology and palaeoecology. Schweizerische Paläontologische Abhandlungen 114: 1–164.
- Bürgin T (1995) Actinopterygian fishes (Osteichthyes; Actinopterygii) from the Kalkschieferzone (Uppermost Ladinian) near Meride (Canton Ticino, southern Switzerland). Eclogae Geologicae Helvetiae 88(3): 803–826.
- Bürgin T (2004) †*Eosemionotus cerasiensis* sp. nov., a new semionotiform fish (Actinopterygii, Halecostomi) from the Middle Triassic Monte San Giorgio

- (southern Switzerland). In: Arratia G, Tintori A, editors. Mesozoic Fishes 3, Systematics, Palaeoenvironments and Biodiversity. Dr. Friedrich Pfeil, München. pp. 239–251.
- Chang M-M, Miao D (2004) An overview of Mesozoic fishes in Asia. In: Arratia, G. & Tintori, A. (eds) Mesozoic Fishes 3. Systematics, Palaeoenvironments and Biodiversity. Dr. Friedrich Pfeil, München. pp. 535–563.
- Clément G (1999) The actinistian (Sarcopterygii) *Piveteauia madagascariensis* Lehman from the Lower Triassic of northwestern Madagascar: A redescription on the basis of new material. Journal of Vertebrate Paleontology 19(2): 234–242.
- Compter G (1891) Ein Beitrag zur Paläontologie des oberen Muschelkalkes. Zeitschrift für Naturwissenschaften 64: 41–61.
- Corroy G (1928) Les vertébrés du Trias de Lorraine et le Trias Lorrain. Annales de Paléontologie 17: 83–136.
- Dames W (1888) Die Ganoiden des deutschen Muschelkalks. Paläontologische Abhandlungen 4(2): 133–180.
- Deecke W (1889) Ueber Fische aus verschiedenen Horizonten der Trias. Palaeontographica 35: 97–138.
- Eck H (1865) Ueber die Formationen des bunten Sandsteins und des Muschelkalks in Oberschlesien und ihre Versteinerungen. Berlin: J.F. Stracke. 148 p.
- Firton F (1934) Description d'une nouvelle espèce de *Saurichthys* du Grès à Voltzia de Wasselonne. Bulletin du Service de la Carte géologique d'Alsace et de Lorraine 2: 89–97.
- Forey PL (1998) History of the coelacanth fishes. London: Chapman & Hall. 419 p.
- Frech F (1903–1908) Lethaea geognostica 2, Das Mesozoicum, 1. Trias. Stuttgart: Schweizerbart'sche Verlagsbuchhandlung. 623 p.
- Frickhinger KA (1991) Fossilien Atlas Fische. Melle: Mergus. 1088 p.

- Furrer, H. (2009) The diet of the predator fish *Saurichthys* from two Middle Triassic Plattenkalk lagerstätten in the Swiss Alps. 5th International Symposium on Lithographic Limestone and Plattenkalk, Basel, Abstracts and Field Guides, 30–31.
- Gall J-C, Grauvogel L, Lehman J-P (1974) Faune du Buntsandstein, V. Les poissons fossiles de la collection Grauvogel-Gall. Annales de Paléontologie 60(2): 129–147.
- Gall J-C, Grauvogel-Stamm L (2005) The early Middle Triassic ‘Grès à Voltzia’ Formation of eastern France: a model of environmental refugium. Comptes Rendus Palevol 4: 637–652.
- Gardiner BG (1960) A revision of certain actinopterygian and coelacanth fishes, chiefly from the Lower Lias. Bulletin of the British Museum (Natural History), Geology 4(7): 239–384.
- Gardiner BG (1988) A new *Cleithrolepis* from the Triassic of central Cyrenaica, northeast Libya. In: El-Arnauti A, Owens B, Thusu B, editors. Subsurface Palynostratigraphy of Northeast Libya. Garyounis University Publications, Benghazi. pp. 259–265.
- Griffith J (1959) On the anatomy of two saurichthyid fishes, *Saurichthys striolatus* (Bronn) and *S. curioni* (Bellotti). Proceedings of the Zoological Society of London 132: 587–606 [doi: 510.1111/j.1469-7998.1959.tb05538.x].
- Guffroy S (1956) Notes paléoichthyologiques. Bulletins de la Société Géologique de France 6: 847–854.
- Herzog A (2001) *Peltoperleidus obristi* sp. nov., ein neuer, kleiner Strahlenflosser (Actinopterygii, Perleidiformes) aus der Prosanto-Formation (Mitteltrias) von Graubünden (Schweiz). Eclogae Geologicae Helvetiae 94: 495–507.

- Herzog A, Bürgin T (2005) A new species of the genus *Besania* Brough 1939 from the Middle Triassic of Canton Grisons (Switzerland) with a discussion of the phylogenetic status of the taxon. *Eclogae Geologicae Helvetiae* 98: 113–122.
- Hilzheimer M (1930) Ein *Saurichthys* Ag. aus dem Röt von Rüdersdorf. *Brandenburgia. Monatsblatt der Gesellschaft für Heimatkunde und Heimatschutz in der Mark Brandenburg* 39: 18–20.
- Hitij T, Tintori A, Žalohar J, Renesto S, Celarc B, Križnar M, Kolar-Jurkovšek T (2010) New fossil sites with Triassic vertebrate fauna from the Kamnik-Savinja Alps, Slovenia. *International Symposium on Triassic and Later Marine Vertebrate Faunas, Beijing. Program and Abstract*: 42–46.
- Hutchinson P (1973) A revision of the redfieldiiform and perleidiform fishes from the Triassic of Bekker's Kraal (South Africa) and Brookvale (New South Wales). *Bulletin of the British Museum (Natural History), Geology* 22(3): 236–354.
- Jin F (2006) An overview of Triassic fishes from China. *Vertebrata Palasiatica* 44: 28–42.
- Jin F, Wang N-Z, Cai Z-Q (2003) A revision of the perleidid fishes from the Lower Yangtze region of south China. *Vertebrata Palasiatica* 41(3): 169–184. [in Chinese with English summary]
- Jörg E (1969) Eine Fischfauna aus dem Oberen Buntsandstein (Unter-Trias) von Karlsruhe-Durlach (Nordbaden). *Beiträge zur Naturkundlichen Forschung in Südwestdeutschland* 28: 87–102.
- Kner R (1866) Die Fische der bituminösen Schiefer von Raibl in Kärnthen. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse* 53: 152–197.

- Kogan I (2011) Remains of *Saurichthys* (Pisces, Actinopterygii) from the Early Triassic Wordie Creek Formation of East Greenland. *Bulletin of the Geological Society of Denmark* 59: 93–100.
- Kunisch H (1885) *Dactylolepis gogolinensis* nov. gen., nov. spec.: *Zeitschrift der Deutschen Geologischen Gesellschaft* 37: 588–594.
- Lambe LM (1914) Description of a new species of *Platysomus* from the neighborhood of Banff, Alberta. *Transactions of the Royal Society of Canada, Series 3, Section 4*, 8: 17–23.
- Lambe LM (1916) Ganoid fishes from near Banff, Alberta. *Proceedings and Transactions of the Royal Society of Canada, Series 3*, 10(4): 35–44.
- Lehman J-P (1952) Etude complémentaire des poissons de l'Eotrias de Madagascar. *Kungliga Svenska Vetenskapsakademiens Handlingar* 4: 1–192.
- Lehman J-P (1953) Etude d'un *Perleidus* du Trias de Madagascar. *Annales de Paléontologie* 39: 3–18.
- Lehman J-P (1956) Compléments à l'étude des genres *Ecrinesomus* et *Bobasatrania* de l'Eotrias de Madagascar. *Annales de Paléontologie* 42: 67–94.
- Lehman J-P, Château C, Laurain M, Nauche M (1959) Paléontologie de Madagascar, 27, Les poissons de la Sakamena moyenne. *Annales de Paléontologie* 45: 175–219.
- Li Q (2009) A new parasemionotid-like fish from the Lower Triassic of Jurong, Jiangsu Province, South China. *Palaeontology* 52: 369–384.
- Lin H, Sun Z, Tintori A, Lombardo C, Jiang D, Hao W (2011) A new species of *Habroichthys* Brough, 1939 (Actinopterygii; Peltopleuriformes) from the Pelsonian (Anisian, Middle Triassic) of Yunnan Province, South China. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 262: 79–89.

- Liu G-B, Feng H-Z, Wang J-X, Wu T-M, Zhai Z-H (2002) Early Triassic fishes from Jurong, Jiangsu [in Chinese with English summary]. *Acta Palaeontologica Sinica* 41: 27–52.
- Lombardo C (1995) *Perleidus altolepis* (Actinopterygii, Perleidiformes) from the Kalkschieferzone of Ca' del Frate (N. Italy). *Géobios* 19: 211–213.
- Lombardo C (2001) Actinopterygians from the Middle Triassic of northern Italy and Canton Ticino (Switzerland): Anatomical descriptions and nomenclatural problems. *Rivista Italiana di Paleontologia e Stratigrafia* 107(3): 345–369.
- Lombardo C, Rusconi M, Tintori A (2008) New perleidiform from the Ladinian (Middle Triassic) of the northern Grigna (northern Italy). *Rivista Italiana di Paleontologia e Stratigrafia* 114(2): 263–272.
- Lombardo C, Sun ZY, Tintori A, Jiang DY, Hao WC (2011) A new species of *Perleidus* (Actinopterygii) from the Middle Triassic of Southern China. *Bollettino della Società Paleontologica Italiana* 50(2): 75–83.
- López-Arbarello A, Sun Z-Y, Sferco E, Tintori A, Xu G-H, Sun Y-L, Wu F-X, Jiang D-Y (2011). New species of *Sangiorgioichthys* Tintori and Lombardo, 2007 (Neopterygii, Semionotiformes) from the Anisian of Luoping (Yunnan Province, South China). *Zootaxa* 2749: 25–39.
- Minikh AV (1981) *Saurichthys* from the Triassic of the USSR [Zaurikhtisy iz triasa SSSR]. *Paleontologicheskii Zhurnal* 1981(1): 105–113. [in Russian]
- Minikh AV (1982) New species of *Saurichthys* from the Early Triassic from the area along the upper Volga [Novye vidy zaurichtisov iz rannego triasa verkhnego Povolzhya]. *Ezhegodnik Vsesoyuzhnogo Paleontologicheskogo Obshchestva* 25: 205–213. [in Russian]
- Moy-Thomas JA (1935) The coelacanth fishes from Madagascar. *Geological Magazine* 72(5): 213–227.

- Müller AH (1969) Über *Dollopterus volitans* (Osteichthyes, Chondrostei), einen Flugfisch aus dem germanischen Oberen Muschelkalk sowie einige Bemerkungen zur Biostratonomie und zur Konkretionsbildung. Freiburger Forschungshefte C 256: 37–46.
- Mutter RJ (2001) The skull of Colobodontidae sensu Andersson 1916 (emended) (Actinopterygii: Perleidiformes). Geologia Insubrica 6(1): 65–78.
- Mutter RJ (2002) Revision of the Triassic family Colobodontidae sensu Andersson 1916 (emended) with a tentative assessment of perleidiform interrelationships (Actinopterygii: Perleidiformes). PhD thesis, University of Zurich, Switzerland. 335 pp.
- Mutter RJ (2004) The “perleidiform” family Colobodontidae: A review. In: Arratia G, Tintori A, editors. Mesozoic Fishes 3, Systematics, Paleoenvironments and Biodiversity. München: Dr. Friedrich Pfeil. pp. 197–208.
- Mutter RJ (2005) Re-assessment of the genus *Helmolepis* Stensiö 1932 (Actinopterygii: Platysiagidae) and the evolution of platysiagids in the Early-Middle Triassic. Eclogae Geologicae Helvetiae 98: 271–280.
- Mutter RJ, Cartanyà J, Basaraba SAU (2008) New evidence of *Saurichthys* from the Lower Triassic with an evaluation of early saurichthyid diversity. In: Arratia G, Schultze H-P, Wilson MVH, editors. Mesozoic Fishes 4 Homology and Phylogeny. München: Dr. Friedrich Pfeil. pp. 103–127.
- Mutter RJ, Herzog A (2004) A new genus of Triassic actinopterygian with an evaluation of deepened flank scales in fusiform fossil fishes. Journal of Vertebrate Paleontology 24(4): 794–801.
- Mutter RJ, Neuman AG (2008) New eugeneodontid sharks from the Lower Triassic Sulphur Mountain Formation of Western Canada. In: Cavin L, Longbottom A,

- Richter M, editors. Fishes and the Break-up of Pangaea Geological Society, London, Special Publications, 295. pp. 9–41.
- Mutter RJ, de Blanger K, Neuman AG (2007) Elasmobranchs from the Lower Triassic Sulphur Mountain Formation near Wapiti Lake (BC, Canada). *Zoological Journal of the Linnean Society* 149: 309–337.
- Mutter RJ, Neuman AG, de Blanger K (2008) *Homalodontus* nom. nov., a replacement name for *Wapitiodus* Mutter, de Blanger and Neuman, 2007 (Homalodontidae nom. nov., ?Hybodontoidae), preoccupied by *Wapitiodus* Orchard, 2005. *Zoological Journal of the Linnean Society* 154: 419–420.
- Neuman AG (1986) Fossil fishes of the families Perleididae and Parasemionotidae from the Lower Triassic Sulphur Mountain Formation of Western Canada. MSc Thesis, Edmonton: University of Alberta. 142 p.
- Neuman AG, Mutter RJ (2005) *Helmolepis cyphognathus*, sp. nov., a new platysiagid actinopterygian from the Lower Triassic Sulphur Mountain Formation (British Columbia, Canada). *Canadian Journal of Earth Sciences* 42: 25–36.
- Nielsen E (1936) Some few preliminary remarks on Triassic Fishes from East Greenland. *Meddelelser om Grønland* 112(3): 1–55.
- Nielsen E (1942) Studies on Triassic fishes from East Greenland 1. *Glaucolepis* and *Boreosomus*. *Palaeozoologica Groenlandica* 1: 1–403.
- Nielsen E (1949) Studies on Triassic fishes from East Greenland 2. *Australosomus* and *Birgeria*. *Palaeozoologica Groenlandica* 3: 1–309.
- Nielsen E (1952) A preliminary note on *Bobasatrania groenlandica*. *Meddelelser fra Dansk Geologisk Förening* 12(12): 197–204.
- Nybelin O (1977) Studies on Triassic fishes from East Greenland III. On *Helmolepis gracilis* Stensiö. *Meddelelser om Grønland* 200(2): 1–13.

- Oertle GF (1927) „*Semionotus letticus* O. Fraas“ und andere Ganoiden aus dem Hohenecker Kalk, von innen gesehen. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B 58: 309–334.
- Oertle GF (1928) Das Vorkommen von Fischen in der Trias Württembergs. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B 60: 325–472.
- Oosterink HW (1986) Winterswijk, geologie 2. De trias-periode (geologie, mineralen en fossielen). Wetenschappelijke Mededelingen van de Koninklijke Nederlandse Natuurhistorische Vereniging 178: 1–120.
- Piveteau J (1934) Paléontologie de Madagascar XXI. – Les poissons du Trias inférieur. Contribution à l'étude des actinoptérygiens. Annales de Paléontologie 23: 83–178.
- Piveteau J (1939–1940) Paléontologie de Madagascar XXIV. – Nouvelles recherches sur les poissons du Trias inférieur. Annales de Paléontologie 28: 71–88.
- Piveteau J (1944-1945) Paléontologie de Madagascar XXV. - Les poissons du Trias inférieur, la famille des Saurichthyidés. Annales de Paléontologie 31: 79–89.
- Priem F (1924) Paléontologie de Madagascar XII. Les poissons fossiles. Annales de Paléontologie 13: 107–132.
- Qian MP, Zhu SP, Zhao FM, Zhou XD, Su R, Gu GH, Zhai ZH (1997) Discovery of Early Triassic fish fossils and its significances in Jurong, Jiangsu Province. Jiangsu Geology 21(2): 65–71. [In Chinese with English abstract]
- Raymond PE (1925) Two new fossil fishes from Alberta. The American Journal of Science 5(9): 551–555.
- Reis OM (1892) Zur Osteologie und Systematik der Belonorhynchiden und Tetragonolepiden. Geognostische Jahreshefte 4: 143–171.

- Rieppel O (1980a) Additional specimens of *Saurichthys madagascariensis* Piveteau, from the Eotrias of Madagascar. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1980(1): 43–51.
- Rieppel O (1980b) A new coelacanth from the Middle Triassic of Monte San Giorgio, Switzerland. Eclogae Geologiae Helvetiae 73(3): 921–939.
- Rieppel O (1982) A new genus of shark from the Middle Triassic of Monte San Giorgio, Switzerland. Palaeontology 25(2): 399–412.
- Rieppel O (1985) Die Triasfauna der Tessiner Kalkalpen 25. Die Gattung *Saurichthys* (Pisces, Actinopterygii) aus der mittleren Trias des Monte San Giorgio, Kanton Tessin. Schweizerische Paläontologische Abhandlungen 108: 1–103.
- Rieppel O (1992) A new species of the genus *Saurichthys* (Pisces: Actinopterygii) from the Middle Triassic of Monte San Giorgio (Switzerland), with comments on the phylogenetic interrelationships of the genus. Palaeontographica Abt A 221: 63–94.
- Romano C, Brinkmann W (2009) Reappraisal of the lower actinopterygian *Birgeria stensioei* ALDINGER, 1931 (Osteichthyes; Birgeriidae) from the Middle Triassic of Monte San Giorgio (Switzerland) and Besano (Italy). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 252: 17–31 [doi: 10.1127/0077-7749/2009/0252-0017].
- Romano C, Brinkmann W (2010) A new specimen of the hybodont shark *Palaeobates polaris* with three-dimensionally preserved Meckel's cartilage from the Smithian (Early Triassic) of Spitsbergen. Journal of Vertebrate Paleontology 30: 1673–1683.
- Romano C, Kogan I, Jenks J, Jerjen I, Brinkmann W (2012) *Saurichthys* and other fossil fishes from the late Smithian (Early Triassic) of Bear Lake County (Idaho,

- USA), with a discussion of saurichthyid palaeogeography and evolution. *Bulletin of Geosciences* 87: 543–570 [doi: 510.3140/bull.geosci.1337].
- Russell LS (1951) *Bobasatrania? canadensis* (Lambe), a giant chondrosteian fish from the Rocky Mountains. *National Museum of Canada Bulletin* 123: 218–224.
- Sander PM, Rieppel OC, Bucher H (1994) New marine vertebrate fauna from the Middle Triassic of Nevada. *Journal of Paleontology* 68(3): 676–680.
- Schaeffer B, Mangus M (1976) An Early Triassic fish assemblage from British Columbia. *Bulletin of the American Museum of Natural History* 156: 515–564.
- Schultze H-P, Möller H (1986) Wirbeltierreste aus dem Mittleren Muschelkalk (Trias) von Göttingen, West-Deutschland. *Paläontologische Zeitschrift* 60(1–2): 109–129.
- Schwarz W (1970) *Birgeria stensioei* Aldinger. In: Kuhn-Schnyder E, Peyer B, editors. *Die Triasfauna der Tessiner Kalkalpen*, X. Schweizerische Paläontologische Abhandlungen, 89. pp. 1–93.
- Stensiö E (1919) Einige Bemerkungen über die systematische Stellung von *Saurichthys mougeoti* Agassiz. *Senckenbergiana* 1(6): 177–181.
- Stensiö E (1921) *Triassic Fishes from Spitzbergen 1*. Vienna: Adolf Holzhausen. 307 p.
- Stensiö E (1925) *Triassic fishes from Spitzbergen 2*. Kungliga Svenska Vetenskapsakademiens Handlingar 3: 1–261.
- Stensiö E (1932) *Triassic fishes from East Greenland 1–2*. *Meddelelser om Grønland* 83(3): 1–298.
- Stolley E (1920) Beiträge zur Kenntnis der Ganoiden des deutschen Muschelkalks. *Palaeontographica* 63: 25–86.
- Su D-Z, Li Z-C (1983) A new Triassic perleidid fish from Hubei, China. *Vertebrata Palasiatica* 21(1): 9–16. [in Chinese with English summary]

- Sun Z-Y, Tintori A, Lombardo C, Jiang D-Y, Hao W-C, et al. (2008) A new species of the genus *Colobodius* Agassiz, 1844 (Osteichthyes, Actinopterygii) from the Pelsonian (Anisian, Middle Triassic) of Guizhou, South China. *Rivista Italiana di Paleontologia e Stratigrafia* 114: 363–376.
- Sun Z-Y, Tintori A, Jiang D-Y, Lombardo C, Rusconi M, et al. (2009) A new perleidiform (Actinopterygii, Osteichthyes) from the middle Anisian (Middle Triassic) of Yunnan, South China. *Acta Geologica Sinica* 83: 460–470.
- Takai F (1976) On *Atherstonia madagascariensis*, a new species of palaeoniscoid fish from Madagascar. *Proceedings of the Japan Academy* 52: 25–28.
- Tanner VM (1936) A study of Utah fossil fishes with the description of a new genus and species. *Proceedings of the Utah Academy of Sciences, Arts and Letters* 13: 81–89.
- Tintori A (1998) *Ctenognathichthys bellottii* (de Alessandri, 1910): Nomenclatural problems and stratigraphical importance of this Middle Triassic actinopterygian fish. *Rivista Italiana di Paleontologia e Stratigrafia* 104(3): 417–423.
- Tintori A, Lombardo C (1999) Late Ladinian fish faunas from Lombardy (North Italy): stratigraphy and paleobiology, In: Arratia G, Schultze H-P, eds) *Mesozoic Fishes 2. Systematics and Fossil Record*. München: Dr. Friedrich Pfeil. pp. 495–504.
- Tintori A, Sun Z-Y, Lombardo C, Jiang D-Y, Sun Y-L, Rusconi M, Hao W-C (2008) New specialized basal neopterygians (Actinopterygii) from Triassic of the Tethys realm. *Geologia Insubrica* 2007(10/2): 13–20.
- Tintori A, Sun Z-Y, Lombardo C, Jiang D-Y, Sun Y-L, Hao W-C (2010) A new basal neopterygian from the Middle Triassic of Luoping County (South China). *Rivista Italiana di Paleontologia e Stratigrafia* 116(2): 161–172.

- Tong J, Zhou X, Erwin DH, Zuo J, Zhao L (2006) Fossil fishes from the Lower Triassic of Majiashan, Chaohu, Anhui Province, China. *Journal of Paleontology* 80: 146–161.
- Wen W, Zhang Q-Y, Hu S-X, Zhou C-Y, Xie T, Huang J-Y, Chen ZQ, Benton MJ (2012) A new basal actinopterygian fish from the Anisian (Middle Triassic) of Luoping, Yunnan Province, Southwest China. *Acta Palaeontologica Polonica* 57(1): 149–160.
- Wen W, Zhang Q-Y, Hu S-X, Benton MJ, Zhou C-Y, Tao X, Huang J-Y, Chen Z-Q (2013) Coelacanths from the Middle Triassic Luoping Biota, Yunnan, South China, with the earliest evidence of ovoviviparity. *Acta Palaeontologica Polonica* 58 (1): 175–193.
- Wendruff AJ, Wilson MVH (2012) A fork-tailed coelacanth, *Rebellatrix divaricerca*, gen. et sp. nov. (Actinistia, Rebellatricidae, fam. nov.), from the Lower Triassic of Western Canada. *Journal of Vertebrate Paleontology* 32: 499–511.
- White EI (1933) New Triassic palaeoniscids from Madagascar. *Annals and Magazine of Natural History, Series 10*, 11: 118–128.
- White EI, Moy-Thomas MA (1940) XLVIII. — Notes on the nomenclature of fossil fishes, 2. Homonyms D–L, *Journal of Natural History, Series 11*, 6(31): 98–103.
- White EI, Moy-Thomas MA (1941) XXV. — Notes on the nomenclature of fossil fishes, 3. Homonyms M–Z, *Journal of Natural History, Series 11*, 7(40): 395–400.
- Wilser JL (1923) *Pygopterus crecelii* n. sp. aus dem Oberen Buntsandstein bei Karlsruhe i. B. *Berichte der Naturforschenden Gesellschaft zu Freiburg i. Br.*, 23(2): 68–78.
- Woodward AS (1895) *Catalogue of the fossil fishes in the British Museum (Natural History)*, Part III. London: British Museum (Natural History). 544 p.

- Woodward AS (1910) On some Permo-Carboniferous fishes from Madagascar. The Annals and Magazine of Natural History, Series 8, 5: 1–6.
- Wu FX, Sun YL, Hao WC, Jiang DY, Xu GH, Sun ZY, Tintori A (2009) A new species of *Saurichthys* (Actinopterygii: Saurichthyidae) from Middle Triassic (Anisian) of Yunnan Province, China. Acta Geologica Sinica [English Edition] 83: 440–450.
- Wu, FX, Sun, YL, Xu GH, Hao WC, Jiang DY, Sun ZY (2011) New saurichthyid actinopterygian fishes from the Anisian (Middle Triassic) of southwestern China. Acta Palaeontologica Polonica 56(3): 581–614.
- Xu, G-H, Wu, F-X (2012) A deep-bodied ginglymodian fish from the Middle Triassic of eastern Yunnan Province, China, and the phylogeny of lower neopterygians. Chinese Science Bulletin 57(1): 111–118.
- Zhang QY, Zhou CY, Lü T & Bai JK (2010) Discovery of Middle Triassic *Saurichthys* in the Luoping area, Yunnan, China. Geological Bulletin of China 29: 26–30. [in Chinese, with English abstract]
- Zhao L-J, Lu L-W (2007) A new genus of Early Triassic perleidid fish from Changxing, Zhejiang, China. Acta Palaeontologica Sinica 46(2): 238–243. [in Chinese with English summary]

Références bibliographiques

- Agassiz L (1833-45) Recherches sur les Poissons Fossiles, Vol. I-V. Neuchâtel: Imprimerie de Petitpierre.
- Albers PCH, Rieppel O (2003) A new species of the sauropterygian genus *Nothosaurus* from the Lower Muschelkalk of Winterswijk, The Netherlands. Journal of Paleontology 77: 738–744.

- Arthaber GV (1924) Die Phylogenie der Nothosaurier. Acta Zoologica (Stockholm) 5: 439-516.
- Bassani F (1886) Sui fossili e sull'età degli schisti bituminosi Triasici di Besano in Lombardia. Comunicazione preliminare. Atti della Società Italiana di Scienze Naturale 29: 15–72.
- Brinkmann W (1998a) Die Ichthyosaurier (Reptilia) aus der Grenzbitumenzone (Mitteltrias) des Monte San Giorgio (Tessin, Schweiz) - neue Ergebnisse. Vierteljahresschrift der Naturforschenden Gesellschaft in Zürich 143: 165–177.
- Brinkmann W (1998b) *Sangiorgiosaurus* n. g. - eine neue Mixosaurier-Gattung (Mixosauridae, Ichthyosauria) mit Quetschzähnen aus der Grenzbitumenzone (Mitteltrias) des Monte San Giorgio (Schweiz, Kanton Tessin). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 207: 125–144.
- Brinkman DB, Zhao X, Nicholls EL (1992) A primitive ichthyosaur from the Lower Triassic of British Columbia, Canada. Palaeontology 35: 465–474.
- Brotzen F (1956) Stratigraphical studies on the Triassic vertebrate fossils from Wadi Raman, Israel. Arkiv for Mineralogi och Geologi 2: 191-217.
- Callaway JM, Brinkman D (1989) Ichthyosaurs (Reptilia, Ichthyosauria) from the Lower and Middle Triassic Sulphur Mountain Formation, Wapiti Lake area, British Columbia, Canada. Canadian Journal of Earth Sciences 26: 1491-1500.
- Carroll RL, Dong Z-M (1991) *Hupehsuchus*, an enigmatic aquatic reptile from the Triassic of China, and the problem of establishing relationships. Philosophical Transactions of the Royal Society of London Series B 331: 131–153.
- Carroll RL, Gaskill P (1985) The nothosaur *Pachypleurosaurus* and the origin of plesiosaurs. Philosophical Transactions of the Royal Society of London Series B 309: 343–393.

- Case EC (1936) A nothosaur from the Triassic of Wyoming. University of Michigan Contributions from the Museum of Paleontology 5: 1–36.
- Chen X, Sander PM, Cheng L, Wang X (2013) A new Triassic ichthyosaur from Yuanan, South China. Acta Geologica Sinica (English Edition) 87(3): 672–677.
- Cheng Y-N, Wu X-C, Sato T, Shan H-Y (2012) A new eosauromorph (Diapsida, Sauropterygia) from the Triassic of China. Journal of Vertebrate Paleontology 32: 1335–1349 [doi: 10.1080/02724634.2012.02695983].
- Cornalia E (1854) Notizie zoologiche sul *Pachypleura edwardsii* Cor. Nuovo sauro acrodonte degli strati triasici di Lombardia. Giornale dell' IR Istituto Lombardo di Scienze, Lettere, ed Arti, Nuova Serie 6: 1–46.
- Cox CB, Smith DG (1973) A review of the Triassic vertebrate faunas of Svalbard. Geological Magazine 110: 405–418.
- Curioni G (1847) Cenni sopra un nuovo saurio fossile dei monti di Perledo sul Lario e sul terreno che lo racchiude. Giornale dell' IR Istituto Lombardo di Scienze, Lettere ed Arti 16: 159–170.
- Cuthbertson RS, Russell AP, Anderson JS (2013) Cranial morphology and relationships of a new grippidian (Ichthyopterygia) from the Vega-Phroso Siltstone Member (Lower Triassic) of British Columbia, Canada. Journal of Vertebrate Paleontology 33: 831–847 [doi: 10.1080/02724634.2013.02755989].
- Dalla Vecchia FM (2004) First record of the rare marine reptile *Thaliodon schmidti* from the Middle Triassic of the Southern Alps. Rivista Italiana di Paleontologia e Stratigrafia 110: 479–492.
- Dal Sasso C, Pinna G (1996) *Besanosaurus leptorhynchus* n. gen. n. sp., a new shastasaurid ichthyosaur from the Middle Triassic of Besano (Lombardy, N. Italy). Paleontologia Lombarda Nuova serie 4: 3–23.

- Dames W (1890) *Anarosaurus pumilio* nov. gen. nov. sp. Zeitschrift der deutschen Geologischen Gesellschaft 42: 74–85.
- Drevermann F (1933) Die Placodontier. 3. Das Skelett von *Placodus gigas* Agassiz im Senckenberg-Museum. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 38: 321–364.
- Edinger T (1921) Über *Nothosaurus*. II. Zur Gaumenfrage. Senckenbergiana 3: 193–205.
- Fraas O (1881) *Simosaurus pusillus* aus der Lettenkohle von Hoheneck. Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg 37: 319–324.
- Fraas E (1896) Die schwäbischen Trias-Saurier nach dem Material der Kgl. Naturalien-Sammlung in Stuttgart zusammengestellt. Festgabe des Königlichen Naturalien-Cabinets in Stuttgart zur 42. Versammlung der Deutschen geologischen Gesellschaft in Stuttgart, August 1896. Stuttgart: E. Schweizerbart'sche Verlagshandlung (E. Koch). 18 p.
- Fritsch KV (1894) Beitrag zur Kenntnis der Saurier des Halle'schen unteren Muschelkalkes. Abhandlungen der Naturforschenden Gesellschaft zu Halle 20: 273–302.
- Fröbisch NB, Sander PM, Rieppel O (2006) A new species of *Cymbospondylus* (Diapsida, Ichthyosauria) from the Middle Triassic of Nevada and a re-evaluation of the skull osteology of the genus. Zoological Journal of the Linnean Society 147: 515–538.
- Geissler G (1895) Ueber neue Saurier-Funde aus dem Muschelkalk von Bayreuth. Zeitschrift der Deutschen Geologischen Gesellschaft 47: 331–355.
- Gürich GJE (1884) Über einige Saurier des oberschlesischen Muschelkalkes. Zeitschrift der Deutschen Geologischen Gesellschaft 36: 125–144.

- Haas G (1959) On some fragments of the dermal skeleton of Placodontia from the Trias of Aarif en Naqa, Sinai Peninsula. Kunglia Svenska vetenskapsakademiens Handlingar Fjärde Serien 7: 1–19.
- Haas G (1963) *Micronothosaurus stensiöi*, ein neuer Nothosauride aus dem Oberen Muschelkalk des Wadi Ramon, Israel. Palaontologische Zeitschrift 37: 161–178.
- Haas G (1980) Ein Nothosaurier-Schädel aus dem Muschelkalk des Wadi Ramon (Negev, Israel). Annalen des Naturhistorischen Museums in Wien 83: 119-125.
- Hänni K (2004) Die Gattung *Ceresiosaurus*. *Ceresiosaurus calgagnii* Peyer und *Ceresiosaurus lanzi* n.sp. (Lariosauridae, Sauropterygia). Zürich: University of Zürich. 146 p.
- Huene Fv (1905) Über die Trias-Dinosaurier Europas. Zeitschrift der Deutschen Geologischen Gesellschaft 57: 345–349.
- Huene Fv (1920) *Gonioglyptus*, ein alttriassischer Stegocephale aus Indien. Acta Zoologica (Stockholm) 1: 433–464.
- Huene Fv (1958) Aus den Lechtaler Alpen ein neuer *Anarosaurus*. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 8/9: 382–384.
- Jiang D-y, Maisch MW, Sun Z-y, Sun Y-l, Hao W-c (2006a) A new species of *Lariosaurus* (Reptilia, Sauropterygia) from the Middle Anisian (Middle Triassic) of southwestern China. Neues Jahrbuch fuer Geologie und Paläontologie, Abhandlungen 242: 19–42.
- Jiang D-y, Maisch MW, Hao W-c, Sun Y-l, Sun Z-y (2006b) *Nothosaurus yangjuanensis* n. sp. (Reptilia, Sauropterygia, Nothosauridae) from the middle Anisian (Middle Triassic) of Guizhou, southwestern China. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 5: 257–276.
- Jiang D-Y, Schmitz L, Hao W-C, Sun Y-L (2006c) A new mixosaurid ichthyosaur from the Middle Triassic of China. Journal of Vertebrate Paleontology 26: 60–69.

- Jiang D-Y, Motani R, Hao W-C, Rieppel O, Sun Y-L, Schmitz L, Sun Z-Y (2008a) First record of Placodontoidea (Reptilia, Sauropterygia, Placodontia) from the Eastern Tethys. *Journal of Vertebrate Paleontology* 28: 904–908.
- Jiang D-Y, Rieppel O, Motani R, Hao W-C, Sun Y-L, et al. (2008b) A new Middle Triassic eosauropterygian (Reptilia, Sauropterygia) from Southwestern China. *Journal of Vertebrate Paleontology* 28: 1055-1062 [doi: 10.1671/0272-4634-1028.1054.1055].
- Jiang D, Motani R, Hao W, Schmitz L, Rieppel O, et al. (2008c) New primitive ichthyosaurian (Reptilia, Diapsida) from the Middle Triassic of Panxian, Guizhou, southwestern China and its position in the Triassic biotic recovery. *Progress in Natural Science* 18: 1315-1319 [doi:1310.1016/j.pnsc.2008.1301.1039].
- Jiang D-Y, Motani R, Tintori A, Rieppel O, Sun Z-Y (2012) Two new Early Triassic marine reptiles from Chaohu, Anhui Province, South China. *Journal of Vertebrate Paleontology, SVP Program and Abstracts Book, 2012*: 117.
- Kelley NP, Motani R, Jiang D-y, Rieppel O, Schmitz A (2012) Selective extinction of Triassic marine reptiles during long-term sea-level changes illuminated by seawater strontium isotopes. *Palaeogeography, Palaeoclimatology, Palaeoecology* [doi: 10.1016/j.palaeo.2012.1007.1026].
- Klein N (2009) Skull morphology of *Anarosaurus heterodontus* (Reptilia: Sauropterygia: Pachypleurosauria) from the lower Muschelkalk of the Germanic Basin (Winterswijk, the Netherlands) *Journal of Vertebrate Paleontology* 29: 665–676 [doi: 610.1671/1039.1029.0327].
- Klein N (2012) Postcranial morphology and growth of the pachypleurosaur *Anarosaurus heterodontus* (Sauropterygia) from the Lower Muschelkalk of Winterswijk, The Netherlands. *Paläontologische Zeitschrift* 86: 389–408 [doi: 310.1007/s12542-12012-10137-12541].

- Klein N, Albers PCH (2009) A new species of the sauropsid reptile *Nothosaurus* from the Lower Muschelkalk of the western Germanic Basin, Winterswijk, The Netherlands. *Acta Palaeontologica Polonica* 54: 589–598 [doi: 510.4202/app.2008.0083].
- Klein N, Scheyer TM (2013) A new placodont sauropterygian from the Middle Triassic of the Netherlands. *Acta Palaeontologica Polonica* [doi: 10.4202/app.2012.0147].
- Koken E (1893) Beiträge zur Kenntnis der Gattung *Nothosaurus*. *Zeitschrift der Deutschen Geologischen Gesellschaft* 45: 337–377.
- Kuhn E (1942) Über einen weiteren Fund von *Paraplocodus broilii* Peyer aus der Trias des Monte San Giorgio. *Eclogae geologicae Helvetiae* 35: 174–183.
- Kuhn-Schwyder E (1959) Ein neuer Pachypleurosaurier von der Stulseralp bei Bergün (Kt. Graubünden, Schweiz). *Eclogae geologicae Helvetiae* 52: 639–658 [doi: 610.5169/seals-162592].
- Kuhn O (1961) Die Familien der rezenten und fossilen Amphibien und Reptilien. Verlagshaus Meisenbach KG, Bamberg. 79p.
- Kuhn-Schwyder E (1987) Die Triasfauna der Tessiner Kalkalpen. XXVI. *Lariosaurus lavizzarii* n. sp. (Reptilia, Sauropterygia). *Schweizerische Paläontologische Abhandlungen* 110: 1–24.
- Lehman J-P (1961) Les Stégocéphales de Madagascar. *Annales de Paléontologie* 47: 42–46.
- Leidy J (1868) Notice of some reptilian remains from Nevada. *Proceedings of the Philadelphia Academy of Sciences* 20: 177–178.
- Li C (2003) First record of protorosaurid reptile (Order Protorosauria) from the Middle Triassic of China. *Acta Geologica Sinica* 77: 419–423.
- Li J-L, Rieppel O (2004) A new nothosaur from Middle Triassic of Guizhou, China. *Vertebrata Palasiatica* 42: 1–12.

- Li J-L, Liu J, Li C, Huang Z-X (2002) The horizon and age of the marine reptiles from Hubei Province, China [in Chinese with English translation]. *Vertebrata Palasiatica* 40: 241–244.
- Li C, Jiang D-Y, Cheng L, Wu X-C, Rieppel O (2013) A new species of *Largocephalosaurus* (Diapsida: Saurosphargidae), with implications for the morphological diversity and phylogeny of the group. *Geological Magazine* [doi: 10.1017/S001675681300023X].
- Li C, Rieppel O, LaBarbera MC (2004) A Triassic aquatic protorosaur with an extremely long neck. *Science* 305: 1931.
- Li C, Rieppel O, Wu X-C, Zhao L-J, Wang L-T (2011) A new Triassic marine reptile from southwestern China. *Journal of Vertebrate Paleontology* 31: 303–312 [doi: 10.1080/02724634.02722011.02550368].
- Li C, Wu X-c, Cheng Y-n, Sato T, Wang L (2006) An unusual archosaurian from the marine Triassic of China. *Naturwissenschaften* 93: 200–206.
- Liu J, Rieppel O, Jiang D-Y, Aitchison JC, Motani R, et al. (2011) A new pachypleurosaur (Reptilia: Sauropterygia) from the lower Middle Triassic of southwestern China and the phylogenetic relationships of Chinese pachypleurosaurs. *Journal of Vertebrate Paleontology* 31: 292–302 [doi: 10.1080/02724634.02722011.02550363].
- Liu J, Motani R, Jiang D-Y, Hu S-X, Aitchison JC, et al. (2013) The first specimen of the Middle Triassic *Phalarodon atavus* (Ichthyosauria: Mixosauridae) from South China, showing postcranial anatomy and peri-Tethyan distribution. *Palaeontology* 56: 849–866 [doi: 10.1111/pala.12021].
- Maganuco S, Steyer JS, Pasini G, Boulay M, Lorrain S, et al. (2009) An exquisite specimen of *Edingerella madagascariensis* (Temnospondyli) from the Lower Triassic of NW Madagascar; cranial anatomy, phylogeny, and restorations.

- Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano 36: 1–72.
- Maisch MW (2010) Phylogeny, systematics, and origin of the Ichthyosauria – the state of the art. *Palaeodiversity* 3: 151–214.
- Maisch MW, Matzke AT (2000) The Ichthyosauria. *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)* 298: 1–159.
- Maisch MW, Matzke AT (2003) Observations on Triassic ichthyosaurs. Part XII. A new Early Triassic ichthyosaur genus from Spitzbergen. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 229: 317–338.
- Mariani E (1923) Su un nuovo esemplare di *Lariosaurus balsami* Cur. trovato negli scisti di Perledo sopra Varenna (Lago di Como). *Atti della Società Italiana di Scienze Naturali* 62: 218–225.
- Massare JA, Callaway JM (1994) *Cymbospondylus* (Ichthyosauria: Shastasauridae) from the Lower Triassic Thaynes Formation of Southeastern Idaho. *Journal of Vertebrate Paleontology* 14: 139–141.
- Maxwell EE, Kear BP (2013) Triassic ichthyopterygian assemblages of the Svalbard Archipelago: a reassessment of taxonomy and distribution. *GFF* 135: 85–94 [doi: 10.1080/11035897.11032012.11759145].
- Mazin J-M (1981) *Svalbardosaurus crassidens* n.g., n.sp., un Ichthyopterygien nouveau du Spathian (Trias inferieur) du Spitzberg. *Comptes Rendus de l'Académie des Sciences, Paris* 293 (2): 203–205.
- Mazin J-M, Bucher H (1987) *Omphalosaurus nettarhynchus*, une nouvelle espèce d'Omphalosauridé (Reptilia, Ichthyopterygia) du Spathien de la Humboldt Range (Nevada, U.S.A.). *Comptes Rendus de l'Académie des Sciences, Paris, Série II* 305: 823–828.

- Mazin J-M, Suteethorn V, Buffetaut E, Jaeger J-J, Helmcke-Ingavat R (1991) Preliminary description of *Thaisaurus chonglakmanii* n. g., n. sp., a new ichthyopterygian (Reptilia) from the Early Triassic of Thailand. *Comptes Rendus de l'Academie des Sciences Paris Série II* 313: 1207–1212.
- McGowan C, Motani R (2003) Ichthyopterygia. *Handbuch der Paläoherpetologie* [Handbook of Paleoherpetology]. München, Germany: F. Pfeil. Part 8: 173p.
- Merriam JC (1906) Preliminary note on a new marine reptile from the Middle Triassic of Nevada. *Bulletin of the Department of Geology at the University of California* 5: 75–79.
- Merriam JC (1910) The skull and dentition of a primitive ichthyosaurian from the Middle Triassic. *University of California Publications, Bulletin of the Department of Geology at the University of California* 5: 381–390.
- Meyer Hv (1842) *Simosaurus*, die Stumpfschnauze, ein Saurier aus dem Muschelkalke von Luneville. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde* 1842: 184–197.
- Meyer Hv (1947-1955) Die Saurier des Muschelkalks mit Rücksicht auf die Saurier aus Buntem Sandstein und Keuper. *Zur Fauna der Vorwelt, zweite Abtheilung*, VIII+ 167 pages. Frankfurt: Heinrich Keller.
- Motani R (1997) Phylogeny of the Ichthyosauria (Amniota: Reptilia) with special reference to Triassic forms. PhD Thesis, Graduate Department of Zoology, Toronto: University of Toronto. 384 p.
- Motani R (1998) First complete forefin of the ichthyosaur *Grippia longirostris* from the Triassic of Spitzbergen. *Palaeontology* 41 (4): 591–599.
- Motani R (2000) Is *Omphalosaurus* ichthyopterygian?--A phylogenetic perspective. *Journal of Vertebrate Paleontology* 20: 295–301 [doi: 210.1671/0272-4634(2000)1020[0295:IOIAPP]1672.1670.CO;1672].

- Motani R, You H (1998) Taxonomy and limb ontogeny of *Chaohusaurus geishanensis* (Ichthyosauria), with a note on the allometric equation. *Journal of Vertebrate Paleontology* 18: 533–540.
- Motani R, Minoura N, Ando T (1998) Ichthyosaurian relationships illuminated by new primitive skeletons from Japan. *Nature* 393: 255–257.
- Motani R, You H, McGowan C (1996) Eel-like swimming in the earliest ichthyosaurs. *Nature* 382: 347–348 [doi:10.1038/382347a382340].
- Müller J (2005) The anatomy of *Askeptosaurus italicus* from the Middle Triassic of Monte San Giorgio and the interrelationships of thalattosaurs (Reptilia, Diapsida). *Canadian Journal of Earth Sciences* 42: 1347–1367 [doi:10.1139/e1305-1030].
- Münster G (1834) Vorläufige Nachricht über einige neue Reptilien im Muschelkalke von Baiern. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde* 1834: 521-527.
- Münster G (1839) Beiträge zur Petrefaktenkunde, mit XVIII nach der Natur gezeichneten Tafeln der Herren Hermann v. Meyer und Professor Rudolph Wagner. Bayreuth: Buchner'sche Buchhandlung.
- Neenan JM, Klein N, Scheyer TM (2013) European origin of placodont marine reptiles and the evolution of crushing dentition in Placodontia. *Nature Communications* 4:1621 [doi: 10.1038/ncomms2633].
- Nicholls EL (1999) A reexamination of *Thalattosaurus* and *Nectosaurus* and the relationships of the Thalattosauria (Reptilia: Diapsida). *PaleoBios* 19: 1–29.
- Nicholls EL, Brinkman DB (1993a) New thalattosaurs (Reptilia: Diapsida) from the Triassic Sulphur Mountain Formation of Wapiti Lake, British Columbia. *Journal of Paleontology* 67: 263–278.

- Nicholls EL, Brinkman D (1993B) A new specimen of *Utatsusaurus* (Reptilia: Ichthyosauria) from the Lower Triassic Sulphur Mountain Formation of British Columbia. Canadian Journal of Earth Sciences 30: 486–490.
- Nicholls EL, Brinkman DB (1995) A new ichthyosaur from the Triassic Sulphur Mountain Formation of British Columbia. In: Sarjeant WAS, editor. Vertebrate Fossils and the Evolution of Scientific Concepts. Amsterdam: Gordon and Breach Publishers. pp. 521–535.
- Nicholls EL, Brinkman DB, Callaway JM (1999) New material of *Phalarodon* (Reptilia: Ichthyosauria) from the Triassic of British Columbia and its bearings on the interrelationships of mixosaurs. Palaeontographica, Abteilung A 252: 1–22.
- Nilsson T (1942) Über einige postkraniale Skelettreste des triassichen Stegocephalen Spitsbergens. Bulletin of the Geological Institution of the University of Uppsala 30: 227–272.
- Nopcsa FB (1925) *Askeptosaurus*, ein neues Reptil der Trias von Besano. Centralblatt für Mineralogie, Geologie und Paläontologie, Abt B: Geologie und Paläontologie 1925: 265–268.
- Nopcsa F (1929) On some nothosaurian reptiles from the Trias. Palaeontological Notes on Reptiles. Geologica Hungarica - Series Palaeontologica Tomus 1 (Fasc 1) [84pp]. pp. 20–44.
- Nosotti S (2007) *Tanystropheus longobardicus* (Reptilia, Protorosauria): re-interpretations of the anatomy based on new specimens from the Middle Triassic of Besano (Lombardy, Northern Italy). Memoire della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano 35: 1–88.
- Nosotti S, Pinna G (1993) *Cyamodus kuhn-schnyderi* n. sp., nouvelle espèce de Cyamodontidae (Reptilia, Placodontia) du Muschelkalk supérieur allemand. Comptes Rendus de l'Academie des Sciences Paris Série II 317: 847–850.

- Nosotti S, Rieppel O (2003) *Eusaurosphargis dalsassoi* n. gen n. sp., a new, unusual diapsid reptile from the Middle Triassic of Besano (Lombardy, N Italy). *Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 31: 3–33.
- Peyer B (1931a) Die Triasfauna der Tessiner Kalkalpen. IV. *Ceresiosaurus calcagnii* nov. gen. nov. spec. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft* 51: 1–68.
- Peyer B (1931b) Die Triasfauna der Tessiner Kalkalpen III. Placodontia. *Abhandlungen der schweizerischen Paläontologischen Gesellschaft* 51: 1–25.
- Peyer B (1931c) *Paraplacodus broilii* nov. gen. nov. sp., ein neuer Placodontier aus der Tessiner Trias. *Centralblatt für Mineralogie, etc Abt B* 10: 570–573.
- Peyer B (1936a) Die Triasfauna der Tessiner Kalkalpen. X. *Clarazia schinzi* nov. gen. nov. spec. *Abhandlungen der schweizerischen Paläontologischen Gesellschaft* 57: 1–61.
- Peyer B (1936b) Die Triasfauna der Tessiner Kalkalpen. XI. *Hescheleria rübeli* nov. gen. nov. spec. *Abhandlungen der schweizerischen Paläontologischen Gesellschaft* 58: 1–48.
- Peyer B (1939) Die Triasfauna der Tessiner Kalkalpen XIV. *Paranothosaurus amsleri* nov. gen. nov. spec. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft* 62: 1–87.
- Peyer B (1955) Die Triasfauna der Tessiner Kalkalpen XVIII. *Helveticosaurus zollingeri* n. g. n. sp. *Abhandlungen der schweizerischen Paläontologischen Gesellschaft* 72: 4–50.
- Quenstedt FA (1852) *Handbuch der Petrefaktenkunde*. Tübingen: H. Laupp. 792 p.
- Renesto S, Pareo M, Lombardo C (2004) A new specimen of the sauropterygian reptile *Lariosaurus* from the Kalkschieferzone (Uppermost Ladinian) of Valceresio

- (Varese N. Italy). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 2004(6): 351–369.
- Rieppel O (1989a) A new pachypleurosaur (Reptilia: Sauropterygia) from the Middle Triassic of Monte San Giorgio, Switzerland. *Philosophical Transactions of the Royal Society of London Series B - Biological Sciences* 323: 1–73.
- Rieppel O (1989b) *Helveticosaurus zollingeri* Peyer (Reptilia, Diapsida) skeletal paedomorphosis, functional anatomy and systematic affinities. *Palaeontographica, Abt A* 208: 123–152.
- Rieppel O (1994) Osteology of *Simosaurus gaillardoti* and the relationships of stem-group Sauropterygia. *Fieldiana (Geology), New Series* 28: 1–85.
- Rieppel O (1997) Revision of the sauropterygian reptile genus *Cymatosaurus* v. Fritsch, 1894, and the relationships of *Germanosaurus* Nopcsa, 1928, from the Middle Triassic of Europe. *Fieldiana: Geology, New Series* 36: 1–38.
- Rieppel O (1998a) *Corosaurus alcovensis* Case and the phylogenetic interrelationships of Triassic stem-group Sauropterygia. *Zoological Journal of the Linnean Society* 124: 1–41.
- Rieppel O (1998b) The systematic status of *Hanosaurus hupehensis* (Reptilia, Sauropterygia) from the Triassic of China. *Journal of Vertebrate Paleontology* 18 (3): 545–557 [doi: 10.1080/02724634.1998.10011082].
- Rieppel O (1998c) The status of the sauropterygian reptile genera *Ceresiosaurus*, *Lariosaurus*, and *Silvestrosaurus* from the Middle Triassic of Europe. *Fieldiana (Geology), New Series* 38: 1–46.
- Rieppel O (1999) The sauropterygian genera *Chinchenia*, *Kwangsisauros*, and *Sanchiaosaurus* from the Lower and Middle Triassic of China. *Journal of Vertebrate Paleontology* 19: 321–337 [doi: 10.1080/02724634.02721999.10011144].

- Rieppel O (2000) Sauropterygia I - Placodontia, Pachypleurosauria, Nothosauroida, Pistosauroida. Handbuch der Paläoherpetologie [Handbook of Paleoherpetology]. München, Germany: F. Pfeil. Part 12A: 134p.
- Rieppel O (2001a) A new species of *Nothosaurus* (Reptilia: Sauropterygia) from the Upper Muschelkalk (Lower Ladinian) of southwestern Germany. *Palaeontographica, Abt A* 263: 137–161.
- Rieppel O (2001b) A new species of *Tanystropheus* (Reptilia: Protorosauria) from the Middle Triassic of Makhtesh Ramon, Israel. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 221: 271–287.
- Rieppel O (2002) The dermal armor of the cyamodontoid placodonts (Reptilia, Sauropterygia): morphology and systematic value. *Fieldiana: Geology, New Series* 46: 1–41.
- Rieppel O, Dalla Vecchia FM (2001) Marine reptiles from the Triassic of the Tre Venezie Area, Northeastern Italy. *Fieldiana: Geology, New Series* 44: 1–25.
- Rieppel O, Hagdorn H (1997) Chapter 5. Paleobiogeography of Middle Triassic Sauropterygia in central and western Europe. In: Callaway JM, Nicholls EL, editors. *Ancient Marine Reptiles*. San Diego, California: Academic Press. pp. 121–144.
- Rieppel O, Hagdorn H (1998) Fossil reptiles from the Spanish Muschelkalk (Mont-Ral and Alcover, Province Tarragona). *Historical Biology* 13: 77–97 [doi: 10.1080/08912969809386575].
- Rieppel O, Lin K (1995) Pachypleurosaur (Reptilia: Sauropterygia) from the Lower Muschelkalk, and a review of the Pachypleurosauroida. *Fieldiana (Geology), New Series* 32: 1–44.
- Rieppel O, Werneburg R (1998) A new species of the sauropterygian *Cymatosaurus* from the Lower Muschelkalk of Thuringia, Germany. *Palaeontology* 41: 575–589.

- Rieppel O, Wild R (1996) A revision of the genus *Nothosaurus* (Reptilia: Sauropterygia) from the Germanic Triassic, with comments on the status of *Conchiosaurus clavatus*. *Fieldiana (Geology)*, New Series No. 34: 1–82.
- Rieppel O, Li C, Fraser NC (2008) The skeletal anatomy of the Triassic protorosaur *Dinocephalosaurus orientalis* Li, from the Middle Triassic of Guizhou Province, Southern China. *Journal of Vertebrate Paleontology* 28: 95–110.
- Rieppel O, Liu J, Li C (2006) A new species of the thalattosaur genus *Anshunsaurus* (Reptilia: Thalattosauria) from the Middle Triassic of Guizhou Province, Southwestern China. *Vertebrata Palasiatica* 44: 285–296.
- Rieppel O, Mazin J-M, Tchernov E (1997) Speciation along rifting continental margins: a new nothosaur from the Negev (Israël). *Comptes Rendus de l'Academie des Sciences Paris, Sciences de la Terre et des Planètes / Earth and Planetary Sciences [Série II a]* 325: 991–997.
- Rieppel O, Mazin J-M, Tchernov E (1999) Sauropterygia from the Middle Triassic of Makhtesh Ramon, Negev, Israel. *Fieldiana (Geology)*, New Series 40: 1–85.
- Rieppel O, Jiang D-Y, Fraser NC, Hao W-C, Motani R, et al. (2010) *Tanystropheus* cf. *T. longobardicus* from the early Late Triassic of Guizhou Province, southwestern China *Journal of Vertebrate Paleontology* 30: 1082–1089 [doi: 10.1080/02724634.02722010.02483548].
- Sander PM (1989a) The pachypleurosaurids (Reptilia: Nothosauria) from the Middle Triassic of Monte San Giorgio (Switzerland) with the description of a new species. *Philosophical Transactions of the Royal Society of London Series B - Biological Sciences* 325: 561–666 [doi: 510.1098/rstb.1989.0103].
- Sander PM (1989b) The large ichthyosaur *Cymbospondylus buchseri*, sp. nov., from the Middle Triassic of Monte San Giorgio (Switzerland), with a survey of the genus in Europe. *Journal of Vertebrate Paleontology* 9: 163–173.

- Sander PM (1997) The paleobiogeography of *Shastasaurus*. In: Callaway JM, Nicholls EL, editors. *Ancient Marine Reptiles*. London: Academic Press. pp. 317–343.
- Sander PM, Faber C (2003) The Triassic marine reptile *Omphalosaurus*: osteology, jaw anatomy, and evidence for ichthyosaurian affinities. *Journal of Vertebrate Paleontology* 23: 799–816 [doi: 710.1671/1676].
- Sander PM, Rieppel OC, Bucher H (1997) A new pistosaurid (Reptilia: Sauropterygia) from the Middle Triassic of Nevada and its implications for the origin of the plesiosaurs. *Journal of Vertebrate Paleontology* 17: 526–533.
- Sanz JL (1983) Los Nothosaurios (Reptilia, Sauropterygia) Espanoles. *Estudios geológicos* 39: 193–215.
- Sato T, Cheng Y-N, Wu X-C, Shan H-Y (2013a) *Diandongosaurus acutidentatus* Shang, Wu & Li, 2011 (Diapsida: Sauropterygia) and the relationships of Chinese eosauropterygians. *Geological Magazine* [doi: 10.1017/S0016756813000356].
- Sato T, Zaho L-J, Wu X-C, Li C (2013) A new specimen of the Triassic pistosauroid *Yunguisaurus*, with implications for the origin of Plesiosauria (Reptilia, Sauropterygia). *Palaeontology* [doi: 10.1111/pala.12048].
- Säve-Söderbergh G (1935) On the dermal bones of the head in labyrinthodont stegocephalians and primitive Reptilia. *Meddelelser om Grønland* 98: 1–211.
- Scheyer TM (2010) New interpretation of the postcranial skeleton and overall body shape of the placodont *Cyamodus hildegardis* Peyer, 1931 (Reptilia, Sauropterygia). *Palaeontologia Electronica* Vol. 13, Issue 2; 15A:15p; http://palaeo-electronica.org/2010_2/232/index.html.
- Schmitz L (2005) The taxonomic status of *Mixosaurus nordenskioeldii*. *Journal of Vertebrate Paleontology* 25: 983–985.

- Schmitz L, Sander PM, Storrs GW, Rieppel O (2004) New Mixosauridae (Ichthyosauria) from the Middle Triassic of the Augusta Mountains (Nevada, USA) and their implications for mixosaur taxonomy. *Palaeontographica Abt A* 270: 133–162.
- Schoch RR, Milner AR (2000) Stereospondyli. *Handbuch der Paläoherpetologie* [Handbook of Paleoherpetology]. München, Germany: F. Pfeil. Part 3B: 220p.
- Schröder H (1914) Wirbeltiere der Rüdersdorfer Trias. *Abhandlungen der Königlich Preussischen Geologischen Landesanstalt, Neue Folge* 65: 1–98.
- Schultze H-P (1970) Über *Nothosaurus*. Neubeschreibung eines Schädels aus dem Keuper. *Senckenbergiana lethaea* 51: 211–237.
- Seeley H (1882) On *Neusticosaurus pusillus* (Fraas), an amphibious reptile having affinities with terrestrial Nothosauria and with marine Plesiosauria. *Quarterly Journal of the geological Society of London* 38: 350–366.
- Sennikov AG (2011) New tanystropheids (Reptilia: Archosauromorpha) from the Triassic of Europe. *Paleontological Journal* 45: 90–104 [Original Russian Text © A.G. Sennikov, 2011, published in *Paleontologicheskii Zhurnal*, 2011, No. 2011, pp. 2082–2096].
- Shang Q-H (2006) A new species of *Nothosaurus* from the early Middle Triassic of Guizhou, China. *Vertebrata Palasiatica* 44: 237–244.
- Shang Q-H, Wu X-C, Li C (2011) A new eosauropterygian from the Middle Triassic of eastern Yunnan Province, southwestern China. *Vertebrata Palasiatica* 49: 155–171.
- Shikama T, Kamei T, Murata M (1978) Early Triassic ichthyosaurus, *Utatsusaurus hataii* gen. et sp. nov., from the Kitakami Massif, Northeast Japan. *Tohoku University, Science Report, 2nd Series (Geology)* 48: 77–97.

- Shishkin MA (1980) The Luzocephalidae, a new Triassic labyrinthodont family [in Russian]. *Paleontologicheskii Zhurnal* [Paleontological Journal] 14: 104–119.
- Steyer JS (2002) The first articulated trematosaur 'amphibian' from the Lower Triassic of Madagascar: implications for the phylogeny of the group. *Palaeontology* 45: 771–793.
- Steyer JS, Boulay M, Lorrain S (2010) 3D external restorations of stegocephalian skulls using ZBrush: the renaissance of fossil amphibians. *Comptes Rendus Palevol* 9: 463–470 [doi: 410.1016/j.crpv.2010.1007.1007].
- Sues H-D, Carroll RL (1985) The pachypleurosauid *Dactylosaurus schroederi* (Diapsida: Sauropterygia. *Canadian Journal of Earth Sciences* 22: 1602–1608.
- Tichy G (1995) Ein früher, durophager Ichthyosaurier (Omphalosauridae) aus der Mitteltrias der Alpen. *Geologisch-Paläontologische Mitteilungen, Innsbruck* 20: 349–369.
- Tintori A, Renesto S (1990) A new *Lariosaurus* from the Kalkschieferzone (uppermost Ladinian) of Valceresio (Varese, N. Italy). *Bollettino della Società Paleontologica Italiana* 29: 309–319.
- Tschanz K (1989) *Lariosaurus buzzii* n. sp. from the Middle Triassic of Monte San Giorgio (Switzerland) with comments on the classification of nothosaurs. *Palaeontographica Abt A* 208: 153–179.
- Wang K (1959) Ueber eine neue fossile Reptilform von Provinz Hupeh, China. *Acta Palaeontologica Sinica* 7: 373–378.
- Watson DMS (1958) A new labyrinthodont (*Paracyclotosaurus*) from the upper Trias of New South Wales. *Bulletin of the British Museum (Natural History), Geology* 3: 233–263.

- Welles SP (1993) A review of the lonchorhynchine trematosaurs (Labyrinthodontia), and a description of a new genus and species from the lower Moenkopi Formation of Arizona. *PaleoBios* 14: 1–24.
- Wiman C (1910) Ichthyosaurier aus der Trias Spitzbergens. *Bulletin of the Geological Institution of the University of Upsala* 10 (1910-1911): 124–148.
- Wiman C (1913) Über das Hinterhaupt der Labyrinthodonten. *Bulletin of the Geological Institution of the University of Upsala* 12: 1–8.
- Wiman C (1914) Über die Stegocephalen aus der Trias Spitzbergens. *Bulletin of the Geological Institution of the University of Upsala* 13 (1915-1916): 1–34.
- Wiman C (1916) Neue Stegocephalenfunde aus dem Posidonomyaschiefer Spitzbergens. *Bulletin of the Geological Institution of the University of Upsala* 13: 209–222.
- Wiman C (1929) Eine neue Reptilien-Ordnung aus der Trias Spitzbergens. *Bulletin of the Geological Institutions of the University of Upsala* 22: 183–196.
- Wild R (1974) E. Kuhn-Schnyder und B. Peyer: Die Triasfauna der Tessiner Kalkalpen. XXIII. *Tanystropheus longobardicus* (Bassani) (Neue Ergebnisse). *Schweizerische Paläontologische Abhandlungen* 95: 1–162.
- Woodward AS (1904) On two new labyrinthodont skulls of the genera *Capitosaurus* and *Aphaneramma*. *Proceedings of the Zoological Society, London* No. 2: 170–176.
- Wu X-C, Li Z, Zhou B-C, Dong Z-M (2003) A polydactylous amniote from the Triassic period. *Nature* 426: 516.
- Wu X-C, Cheng Y-N, Li C, Zhao L-J, Sato T (2011) New information on *Wumengosaurus delicatmandibularis* Jiang et al., 2008 (Diapsida: Sauropterygia), with a revision of the osteology and phylogeny of the taxon.

- Journal of Vertebrate Paleontology 31: 70–83 [doi: 10.1080/02724634.02722011.02546724].
- Young CC (1958) On the new Pachypleurosauroidea from Keichow, South-West China. *Vertebrata PalAsiatica* 2: 69–81.
- Young CC (1959) On a new Nothosauria from the Lower Triassic beds of Kwangsi. *Vertebrata PalAsiatica* 3 (2): 73–79.
- Young CC (1965) On the new nothosaurs from Hupeh and Kweichow, China. *Vertebrata PalAsiatica* 9: 337–356.
- Young CC (1972) A marine lizard from Nanchang, Hupeh province. *Memoirs of the Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica* 9: 17–28.
- Young CC, Dong ZM (1972) On the Triassic aquatic reptiles of China. *Institute of Vertebrate Paleontology and Palaeoanthropology, Chinese academy of Science, memoir* 9: 1–34.
- Zhao L-J, Li C, Liu J, He T (2008) A new armored placodont from the Middle Triassic of Yunnan Province, southwestern China. *Vertebrata PalAsiatica* 46: 171–177.